YIELD-LIMITING PROCESSES IN COWPEA (*VIGNA UNGUICULATA* (L.) WALP.) CULTIVAR VITA-5

© John F. Argall

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science

Department of Plant Science
Macdonald Campus
McGill University
Montreal

August 1983

Abstract

M.Sc. John F. Argall Plant Science

Yield-limiting processes in cowpea

(Vigna unguiculata (L.) Walp.)

cultivar Vita-5

Studies were undertaken to better define yield-limiting processes associated with the low functional activity of cowpea (Vigna unguiculata (L.) Walp.) peduncles.

Twenty-two cultivars were examined in order to assess peduncle activity. For the cultivar Vita-5, in which 60% of the peduncle sites did not remain productive, studies on suspected yield-limiting processes were conducted.

Chemical and mechanical treatments aimed at modifying apical dominance were performed and had favorable effects on agronomic yield.

A model of competitive inhibition between reproductive units was also proposed. It was observed that a competitively strong reproductive sink could divert large amounts of ^{14}C assimilates from a source generally associated with another reproductive unit.

The implications of these findings for crop improvement are discussed.

Resumé

M.Sc. John F. Argall Plant Science

Des étapes limitantes au rendement dans le Vigna unguiculata (L.) Walp. cultivar Vita-5

Ces études ont été conduites afin de mieux définir les processus physiologiques reliés aux activités fonctionelles des pédoncules du Vigna unguiculata (L.) Walp. en tant que facteur limitant du rendement.

Vingt-deux cultivars ont été examinés pour determiner l'activité pédonculaire. Pour le cultivar Vita-5, 60 % des sites pédonculaires sont demeurés improductifs. Des études sur les processus susceptibles d'être limitant ont été realisées. Des traitement chimiques et mécaniques visant à modifier la dominance apicale ont produit des éffets favorable sur le rendement agronomique.

Un model d'inhibition compétitif entre des unités réproductives a été proposé. Il a ete observé qu'un 'puit' fortement compétitif pouvait mobiliser d'importantes quantités d'assimilats de ^{14}C d'une source associé a une autre unité reproductive.

La discussion porte aussi sur l'application des resultats obtenus en vue d'ameliorer les rendements de cette culture.

ACKNOWLEDGEMENTS

I am grateful to those people who have contributed to the preparation of this thesis, particularly Dr. K. A. Stewart, a most understanding advisor and a good friend.

I acknowledge my appreciation to fellow students: Pierre-Alain Blais, of the McGill University Biology Department, for assistance and guidance with the photosynthesis apparatus; Shahrokh Khanizadeh, for assistance in dealing with the computer; and numerous other friends and colleagues whose eager advice and assistance was greatly appreciated. I also wish to thank Dr. R.-L. Pelletier and Dr. D. Buszard for acting as members of my advisory committee.

Special recognition is extended to Ms. Marion Rigby for assistance with the preparation of the manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

ABBREVIATIONS USED

Abbreviation	Term represented
BA	6-benzyladenine (or benzyladenine)
^{14}C	radioisotope carbon-14
cv.	cultivar
C.V.	coefficient of variability
df	degrees of freedom
F	F value
H.I.	Harvest Index
IAA	indole-3-acetic acid
MS	mean square
^{32}P	radioisotope phosphorus-32
Prob	probability
rep	replicate
SS	sum of squares
TIBA	2,3,5-triiodobenzoic acid
Trt	treatment
WP	wettable powder

1. INTRODUCTION

Protein is one of the major components of human nutrition. Inadequate intake of this dietary component is a major cause of malnutrition, and its continued absence can result in serious illnesses. In developing countries, plants represent a very important source of protein, mainly because adequate intake of animal protein is limited by the financial means of a large part of rural populations (El Baradi, 1975).

As a source of human food, grain legumes (or pulses) are second only to cereals, and are nutritionally two to three times richer in protein. Consequently , they have contributed enormously over the centuries to balancing diets high in cereals and starchy foods. As dietary components, these crops generally have amino acid profiles which are complementary to those of rice, corn, and other cereal grains; and, in the case of tuber/ root-based diets, grain legumes are known to provide virtually the sole source of available protein. In a protein hungry world, the grain legumes are obvious candidates for increasing the production of plant protein.

This fact is well recognized by the FAO, who, in the Provisional Indicative World Plan for Agricultural Development, stressed the vital importance of increasing the output of cheaper sources of quality protein and the immediate potential of grain legume crops for filling this need (Summerfield et al., 1974). The importance of the pulses, and legume crops in general, is rendered even more evident in light of their use of nitrogen-fixing bacteria to meet their needs for nitrogen

without fertilizers.

Multipurpose crop plants abound in the Leguminosae (Isley, 1982). They are most commonly consumed as mature dry seeds (pulses), but some of these same species are also eaten as immature green seeds or as greens pods with the seeds enclosed. Some grain legumes - such as soybeans, peanuts, and winged beans - are also rich in oil. Still others have leaves which may serve as a pot herb or green fodder (National Academy of Sciences, 1979).

The cowpea (Vigna unguiculata (L.) Walp.) is one such crop. It is an ancient neolithic crop grown throughout the tropics and subtropics as a pulse, a vegetable, a pot herb, for fodder, and as a cover crop (Purseglove, 1968; Rachie and Roberts, 1974; Summerfield et al., 1974; Steele and Mehra, 1978). Throughout Africa, cowpeas are generally used as an ingredient in thick soups or gruel with other vegetables, in fried or steamed bean cakes, or in various other regionally preferred preparations (Summerfield et al., 1974).

In all African diets in which they are used, cowpeas are important for their nutritive value. Johnson and Raymond (1964) report that the mature seeds of cowpea contain on average 12% water, 23-24% protein, 0.7-1% oil, 18% fibre, and 57-88% carbohydrates. Summerfield et al. (1974) report that the percentage protein in cowpea seeds varies between 19 and 26 percent, with upper limits of up to 35% having been reported.

As with most seed legumes, cowpea is deficient in sulfur-containing amino acids. With appropriate complementation/ supplementation, however, it is possible to raise the protein value to 95% that of egg albumen (Boulter et al., 1973). In terms of amino acid complementation,

the high lysine content of cowpea seed is very important in low-lysine cereal-based diets. The role of cowpea is even more vital, however, in the protein-deficient root and tuber diets of humid Africa. It compares favorably to protein of animal origin, with an adjusted protein content of 15% - a value used by Schmitt (1979) in estimating the contributions of individual food items to total protein supply, using FAO/WHO amino acid scores. In addition to their importance as an energy source and a source of protein, cowpeas are also important for their calcium (90mg/100g), iron (6-7mg/100g), nicotinic acid (2mg/100g) and thiamin (0.9mg/100g) contents (Platt,1962).

The cowpea is chiefly important in African cereal-farming systems where the mature pods, young leaves, and pods are eaten, while the haulms are fed to livestock. In this context, they are often intercropped with sorghum or pearl millet (Steele and Mehra, 1978; Summerfield et al., 1974). Modern centres of dry seed production include West Africa (primarily Nigeria), India, and Brazil; while low agronomic productivity and labour-intensive harvesting have led to its replacement by more easily harvested species of greater productivity in the USA (Wolfe and Kipps, 1959).

In all areas of production, seed yields of cowpea have always been inconsistent and this has been thought to be due mainly to variations in the proportion of reproductive structures that actually reach the mature pod stage (Summerfield et al., 1974). Ojehomon (1968b) reports that 70-80% of buds are shed before anthesis. Flower abortion is also considered to be responsible for a considerable decrease in seed yield (Ojehomon, 1968a, 1968b, 1972). Though the plant has the ability to

compensate for flower loss by the setting of more buds, the scope of recovery appears to be limited (Ojehomon, 1970).

This phenomenon is in no way restricted to cowpea, however. The food legumes are notorious for their profligate loss of flower buds, flowers, and young pods, even under the most sophisticated agronomic conditions. This abscission during the flowering and fruiting period in the grain legumes is often greater than 50%. In soybean (Glycine max (L.)Merr.), the most widely studied grain legume, the total reproductive abscission has been shown to range as high as 81% and commonly well over 60% (Van Schaik and Probst, 1958a,1958b; Hardman, 1970; Brevedan et al., 1978; Hansen and Shibles, 1978; Wiebold et al., 1981).

Observations of a comparable order of magnitude have been made for a number of grain legume species of both temperate and tropical adaptation : Arachis hypogea (peanut) (Smith,1954; Ishag, 1970); Cajanus cajan (pigeon pea) (Narayanan and Sheldrake, 1976); Cicer arietinum (chickpea) (Saxena and Sheldrake, 1976); Phaseolus vulgaris (field beans) (Webster et al., 1975; Graham, 1978); Vicia faba (broad bean) (Lawes, 1974; El-Beltagy and Hall, 1975); Vigna mungo (mung bean) (Sinha, 1977).

A great deal of research effort has been directed toward determining the causes and controls of premature abscission of legume flowers and fruits (among others, Van Steveninck, 1957; Ojehomon, 1968a, 1968b, 1970, 1972, 1975; Weigle et al., 1973; Webster et al., 1975; Adedipe et al., 1976; Huff and Dybing, 1980; Okelana and Adedipe, 1982). Overall, it would appear that such flowers and young fruits may be lost because a large proportion of assimilates are sequestered by earlier formed fruits

(Adedipe et al., 1976; Tamas et al., 1979b). Several studies appear to indicate that abortion and abscission are not inherent characteristics of later-formed buds, flowers, and fruits, however, since these will generally become reproductive if earlier-formed flowers or pods are removed (Van Stevenick, 1957; Ojehomon, 1970; Sinha, 1977). Rather it seems that later-formed reproductive structures are developed to offset losses of reproductive productivity which might occur due to loss of earlier-formed pods (from insect predation, for example). When successful development in earlier-formed fruits does occur, however, these fruits appear to produce chemical signals which promote the abortion of younger reproductive structures, particularly when these are in the same inflorescence (Van Stevenick, 1957, 1958, 1959; Tamas et al., 1979a; Huff and Dybing, 1980). A regulatory influence of older fruits on the abscisic acid content of younger fruits has been suggested, for example (Porter and Van Stevenick, 1966; Tamas et al., 1979a), though there are reports that these concentrations of ABA may not be related entirely to the degree of organ shedding per se (Porter, 1977).

Regardless of the mechanism, however, it is accepted that the period of anthesis and pod set in grain legumes is indeed characterized by an abundant loss of flower buds, open flowers, and immature pods (Summerfield and Wien, 1980). Further, several reports relate this to a number of genetic and environmental variables: crop variety, (Van Schaik and Probst, 1958a; Adedipe and Ormrod, 1975) soil moisture, (Stewart, 1976) temperature, and photoperiod (Van Schaik and Probst, 1958b; Ojehomon et al., 1968; Stewart, 1976). In general, it appears

warm (>30°C) or cool (<15°C) air temperatures, a dry atmosphere, water stress, and, for short day species, long photoperiods, are particularly unfavorable during anthesis and pod set (Stewart et al., 1980).

Despite the obvious loss of yield from abscised flower buds, flowers, and young pods in cowpea, it has been suggested that an unjustified bias in research activity has been focused on this loss in 'theoretical yield potential' - the characterization of which may be of only limited practical significance in the realization of yield potential (Summerfield et al., 1983). It is in fact true that legume yields depend upon both vegetative and reproductive components, as outlined in Figure 1. In more or less determinate cultivars of cowpea, the contribution of some of these components to ultimate seed yield are determined by the time the plants come into first flower (phenological potential). Hence, it has recently been suggested that these components may be equally, if not more, important in yield analysis, though they are very seldom referred to (Summerfield op cit.,).

The recent findings of Stewart et al. (1980)lend support to such a view, at least for determinate cowpea. In environments conducive to either small, intermediate, or very large seed yields (range 42-98 g/plant) these workers demonstrated that there was little variation in the likelihood of premature abscission of flowers from specific points on an inflorescence. Further, the premature abscission of flowers and immature pods did not appear to be the most important factor limiting yield accretion in general.

1. Number of nodes per plant (N) -> Vegetative growth x duration of pre-flowering period
2. % of N which become and remain reproductive

(1 x 2) = PHENOLOGICAL POTENTIAL

3. Number of flowers per reproductive node (F)) Number of pods per
4. % of F which set pods) reproductive node (P)
5. % of P which are retained
6. Number of seeds per pod (S)

(3 x 4 x 5 x 6) = REPRODUCTIVE EFFICACY

7. % of S which attain maturity <-----> Carbon and nitrogen supply
8. Mean seed weight -----> Mean seed growth rate x duration of pod-fill

7 x 8 = YIELD CULMINATION

Therefore yield per plant = (1 x 2) x (3 x 4 x 5 x 6) x (7 x 8)

Figure 1. Components of seed yield in more or less determinate legumes (After Summerfield and Wien, 1980).

Some of these findings are presented in Table 1. Averaged over all treatment combinations, the premature abscission of peduncles (a function of the number of vegetative nodes which become reproductive) reduced yield potential by about one third, while the loss of open flowers and immature pods, taken separately, did not incur as great a loss (23 and 16 percent, respectively). This was shown to be particularly true of those plants which were grown in environments particularly unfavorable for seed yield (33/19^{o}C at both daylengths). In these instances peduncle abscission contributed over 50% of the loss in theoretical yield potential, while losses due to the subsequent loss of reproductive structures was much lower.

Table 1. Effects of environmental treatment combinations on the cumulative loss of yield potential (%) after successive stages of development (means of 6 replicates)*

Cumulative loss of yield potential from reproductive nodes	Daylength and day/night temperatures(°C)							
	11 h 40 min				13 h 20 min			
	27/19	27/24	33/19	33/24	27/19	27/24	33/19	33/24
Reproductive nodes	100	100	100	100	100	100	100	100
Peduncle abscission	78.7	81.0	45.1	67.7	75.8	77.1	47.1	54.9
Peduncle + flower abscission	69.5	52.9	20.6	41.4	49.9	44.2	21.1	37.2
Peduncle+flower+pod abscission	36.9	30.3	10.5	26.8	32.5	27.4	18.0	23.0
Seed yield(g/plant)	86.0	68.0	42.0	67.2	97.2	64.0	44.0	65.1

* loss of reproductive potential calculated relative to the yield which would have been produced if all the nodes that became reproductive on plant in different regimes (a yield potential of 100% in each case) had retained all their peduncles, open flowers, and immature pods. (from Stewart et. al., 1980)

In light of these observations, the present investigations were undertaken to obtain a better understanding of the phenological potential and the processes which underlie its expression. The first experiment was a screening of cowpea cultivars, designed in order to assess the severity of peduncle inactivity and to determine a baseline for further investigation.

2. EXPERIMENT 1: CULTIVAR SCREENING

2.1 Introduction

To assess various aspects of the phenological potential in cowpea, a cultivar screening was performed. To facilitate comprehension of the work undertaken, an introduction to the plant is presented.

2.1.1 The plant Cultivated cowpeas are glabrate annual legumes of diverse growth habits, variously described as erect, semi-erect, shrubby, trailing, prostrate, and climbing. Their germination is epigeal, though the cotyledons do not persist. Following germination, the primary leaves which are present in the dormant embryo emerge as a pair of simple, entire, opposite leaves. These are followed by alternate, pinnately trifoliate leaves composed of shortly-stalked leaflets, 5-18 cm long and 3-16 cm wide, which are linear, lanceolate, or broadly or narrowly ovate in shape, generally entire, and broadly cuneate or rounded at the base, with the leaflets gradually tapering to a pointed tip (Steele and Mehra, 1978). Each leaf has three buds in its axil, and, unless early growth is injured, only the central bud expands to produce either a potentially indeterminate, monopodial branch or a racemose inflorescence. In general, branches will grow out from the axils of the pair of simple, opposite leaves and the first two or three trifoliate leaves of the seedling.

2.1.2. The inflorescence Where an inflorescence develops, it is a compound raceme composed of several modified simple racemes (Ojehomon, 1968a) on a 10–25 cm (up to 50 cm) peduncle. Each simple raceme has 6–12 flower buds, but only the oldest pairs develop, leaving the remainder to degenerate and produce a 'cushion nectary' which is visible between the two flowers of each simple raceme. The peduncle tip as a compound raceme is seen as a swollen axis rarely longer than 2.5 cm long which bears five or six alternate flower sets arranged in acropetal order. Only two or three flowers in each compound raceme typically set fruits, while many flower buds, open flowers, and immature pods are shed (Ojehomon, 1968b).

When floral primordia develop, the pattern is rather distinct: (a) primordia expansion; (b) emergence of the corolla tip above the calyx; (c) expansion of the corolla into a tightly closed green structure; (d) change of the corolla from green to white/ mauve/ pale yellow; (e) anthesis; (f) petal collapse; (g) discarding of the corolla (generally within twenty-four hours of anthesis) (Figure 2).

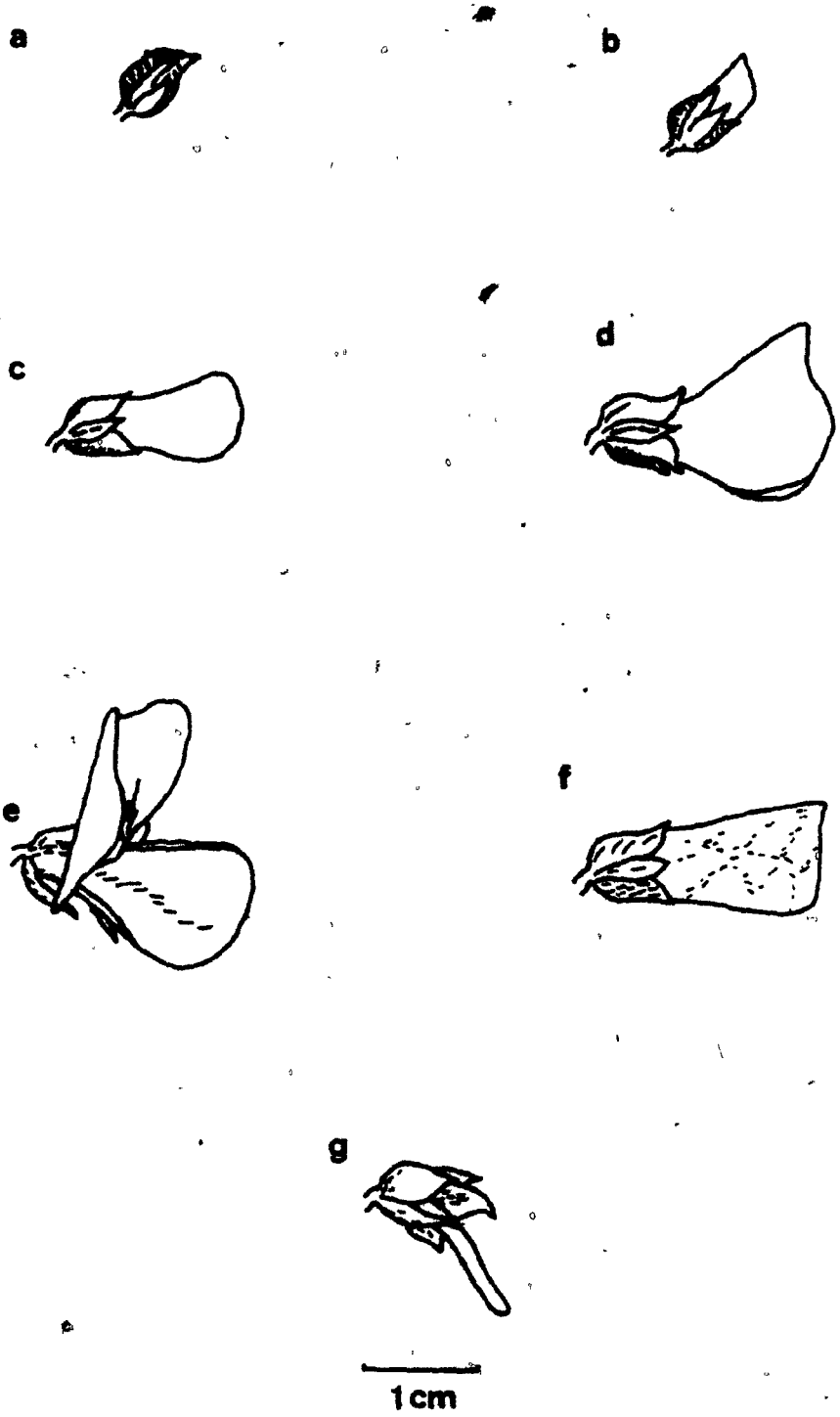
Most cultivars produce non-dehiscent pods 12-20 cm long and these are diverse in colour and shape, as are the seeds which they contain when they mature (Steele and Mehra, 1978).

Figure 2

Diagrammatic representation of the development of a single flower bud of cowpea

(legend a-g, see text)

(from Stewart, 1976)


a
b
c
d
e
f
g
1 cm

2.2 Materials and Methods

2.2.1 Plant material and environmental control In the summer of 1980, a greenhouse screening of several of the current best cowpea cultivars (arising from Nigerian cowpea breeding programs and obtained from the International Institute of Tropical Agriculture, Ibadan) was performed. The plants were grown in an environment simulating their lieu of selection, using many of the husbandry and management techniques previously described for the growing of this species under simulated tropical conditions in controlled environments (Huxley and Summerfield, 1976; Summerfield et al., 1977). As these workers point out, such environmental controls in crop physiology experiments are mandatory in order to yield findings which are useful as an adjunct to field research, with plants closely resembling those grown in tropical fields in terms of reproductive ontogeny and overall morphology (Summerfield et al., op. cit.).

All plants were hence grown at the mean values of daylength and meteorological screen day and night temperatures of the main growing season at Ibadan, Nigeria (from Huxley and Summerfield, 1976). The whole screening was conducted in the same section (floor area 6.4 x 7.7 m; 3.7 m high) of a compartmentalized Standard 'Lord and Burnham' glasshouse. The plants were maintained as nearly as possible at a day/night temperature regime of 30 ($\pm 5^{o}C$)/ 21($\pm 1^{o}C$), a twelve hour thirty minute daylength, and a relative humidity of 70 (± 10)%. The dark period was achieved by use of blackout curtains, while humidity was kept high by periodic flooding of the greenhouse floor and spraying of the

greenhouse walls.

2.2.2 Plant husbandry All plants were grown in 18-cm diameter plastic pots containing a drainage layer of clay chips and a John Innes Potting Compost no. 1 (Bunt, 1976). The mediumwas soaked with water twenty-four hours prior to the sowing of three uninoculated seeds per pot. Seven days after emergence, the plants were thinned to one per pot and fertilized then, and once weekly thenceforth, with a water-soluble commercial grade formulation (10-10-10), yielding 300 ppm of nitrogen per application. Plants were staked and tied as necessary.

2.2.3 Pest control In terms of pest control, the following measures were exercised in order to minimize the effects of extraneous factors on data variability:

(a) All pots were soaked in a mild chlorine solution (5% bleach) one hour, allowed to dry, then rinsed and dried prior to use;

(b) All benches used were scrubbed with a mild chlorine solution (5% bleach) prior to use;

(c) Populations of the common glasshouse pest, red spider mite (Tetranychus urticae Koch.) were kept in check by scheduled applications of Pentac 50%WP (miticide).

2.2.4. Experimental design and data collection All treatments (cultivars) were laid out in two blocks in a randomized complete block design against a possible north/south light gradient. Plant ontogeny was monitored daily by recording (from emergence through to maturity) the following characteristics: node appearance (that is, when the leaf subtending a given node expanded); peduncle appearance at a given node; flowering at a given peduncle site; fruit set at a given peduncle site; and, when appropriate, the onset and actual abscission of a peduncle (Plate 1); in addition to the days to emergence, first anthesis, and harvest. Yield data were also taken.

Analyses of variance were performed on all variables and Duncan's multiple range tests were performed on selected variables.

Plate 1

Developmental stages of cowpea plants

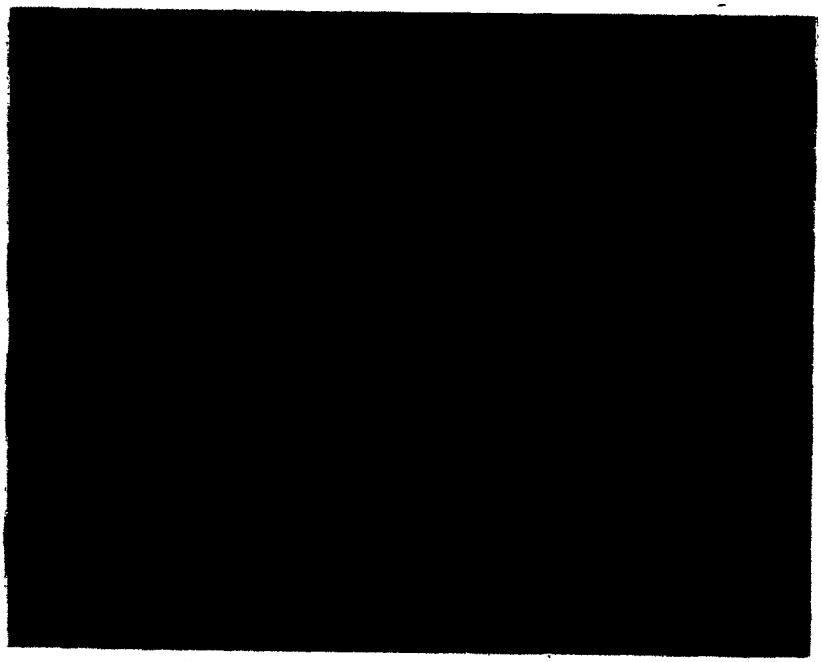
1a - node appearance (with an arrow pointing to the recently expanded leaf)

1b - peduncle appearance at a given node (with an arrow pointing to the elongating peduncle)

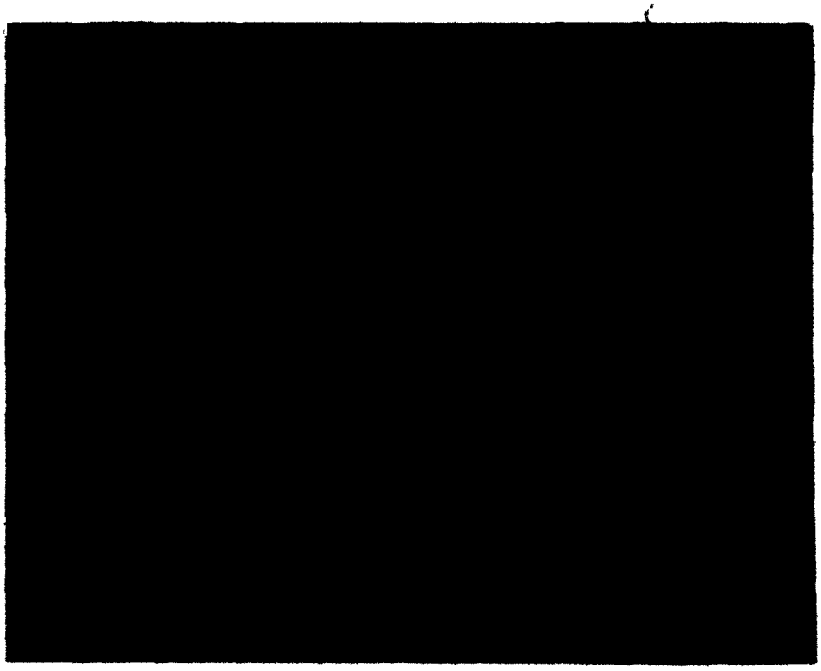
1c - apex of a cowpea peduncle showing (left to right) a young pod, two flowering sites and a mature flower

1d - abscission of a young cowpea peduncle (with an arrow pointing to the abscission layer)

a

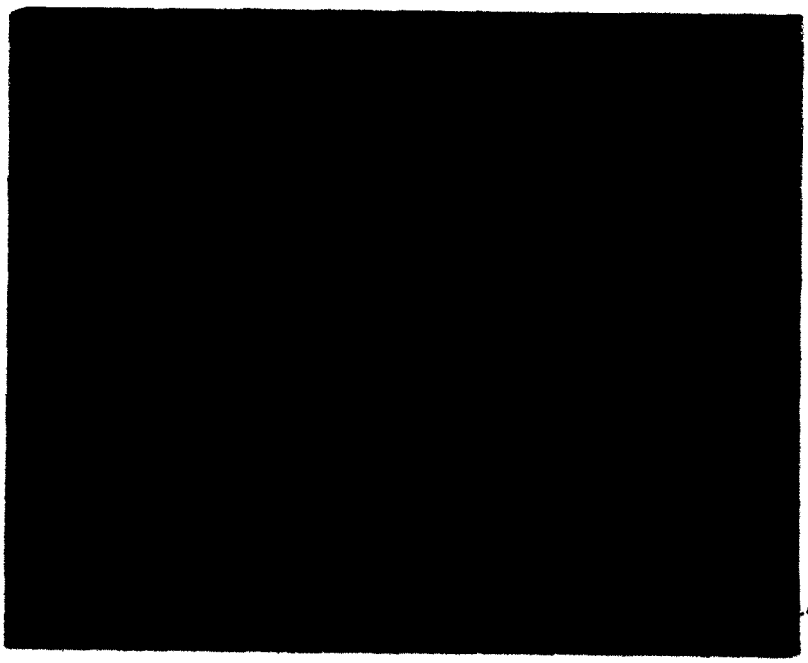


b



c

d



2.3 Results and discussion

For the plant attributes recorded, significant differences among cultivars were observed (Table 2). The differences were less acute for the earliest growth stage (emergence) but even this was significant ($p<0.02$). A block effect was noted only in the case of the more variable traits (peduncle number and the percentage of non-functional peduncle sites).

Table 2. Significance levels of several plant atrributes for twenty-two cultivars of cowpea (Vigna unguiculata (L.) Walp.)

Plant attribute	Prob > F		C.V.
	Variety	Block	(%)
Days to emergence	0.02	0.28	15.0
Days to anthesis	0.01	0.82	5.3
Days to harvest	0.01	0.49	4.5
Peduncle number	0.01	0.01	17.2
Percent non-functional peduncle sites*	0.01	0.02	20.8
Pods per plant	0.01	0.37	12.6
Seeds per pod	0.01	0.04	12.1
Mean seed weight (mg)	0.01	0.47	9.0
Seed weight (g/plant)	0.01	0.63	14.5

* represent those sites which, though becoming reproductive, fail to contribute to yield.

To exemplify the differences between cultivars, a number of plant attributes are presented (Table 3). For example, a 3 day, 17 day, and 33 day difference was noted between extremes for days to emergence, first anthesis, and harvest, respectively. Yields, expressed as grams per plant, varied substantially from a low of 13.4 (for cv. TVu 76) to a high of 41.2 (for cv. Vita-3). Most important for this study, however, was the percentage of non-functional reproductive sites, which represents those sites which though becoming reproductive, failed to contribute to yield. For the majority of cultivars, it is obvious that very few of the potential reproductive sites managed to contribute to yield. This was especially pronounced for such cultivars as Vita-5 and TVx1836-013J, which were found to have a non-functional status for up to 60% of their peduncles. Based on the findings, the variety with the greatest percentage of non-functional peduncle sites (Vita-5) was chosen for further study.

Vita-5 is described by the International Institute of Tropical Agriculture (I.I.T.A.) as a moderately high-yielding cultivar with exceptionally good tolerance or resistance to major diseases and insects. Its creamy white seeds are of size class 5 (small to medium size), with above average protein quality, average protein content, and very good consumer acceptability. The variety begins flowering 42 days after planting under field conditions, which compares fairly well with the number of days recorded here, suggesting a fairly accurate environmental simulation.

Table 3. Selected plant attributes for twenty-two cultivars of cowpea (Vigna unguiculata (L.) Walp.).

Cultivar	Days to Emergence	Days to anthesis	Days to Harvest	Yield (g/plant)	% N.F. ped. sites
Vita 5	4 c	47 fgh	84 cde	16.8 hi	60 a
TVx1836-013J	5 abc	48 efgh	78 defg	19.9 fghi	59 a
TVx1999-02E	6 abc	52 cdef	78 defg	27.8 bcdef	46 a
TVx1948-01E	4 c	47 fgh	78 defg	21.8 defgh	45 ab
Vita-3	4 c	60 a	104 a	41.2 a	45 ab
TVx2907-02D	4 c	56 abc	93 b	35.5 ab	43 bc
TVx66-2H	4 c	55 abcd	85 cd	24.2 defgh	40 bcd
TVx2949-01D	6 abc	48 efgh	87 bc	29.9 bcd	39 bcde
TVx1850-01E	5 abc	52 cdef	77 defg	19.1 ghi	38 bcde
TVu 76	5 abc	47 fgh	77 defg	18.3 hi	37 bcde
Ife-Brouen	6 ab	48 efgh	82 cdef	19.9 fghi	35 bcde
TVx289-46	7 a	59 ab	83 cde	33.4 bc	33 bcde
TVx1999-01F	4 c	48 efgh	77 defg	21.9 defgh	30 bcdef
TVx2939-09D	4 c	44 h	80 cdefg	28.9 bcde	28 cdefg
TVx3218-02D	4 c	50 cdefg	76 efg	22.4 defgh	27 cdefg
TVu 76	4 c	44 h	71 g	13.4 i	26 defg
TVx2912-011D	5 abc	54 bcde	84 cde	25.3 defgh	26 defg
TVx7-4K	5 bc	51 cdef	77 defg	20.6 efghi	23 efg
Vita-4	5 abc	52 cdef	79 cdefg	27.1 cdefgh	17 fgh
TVx1576-01E	4 c	47 fgh	76 defg	22.4 defgh	16 fgh
TVx33-1J	4 c	49 defgh	80 cdefg	22.6 defgh	13 gh
TVx3048-02D	4 c	45 gh	73 fg	17.4 hi	5 h

% N. F. = % non-functional
Figures represent the means of two observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05

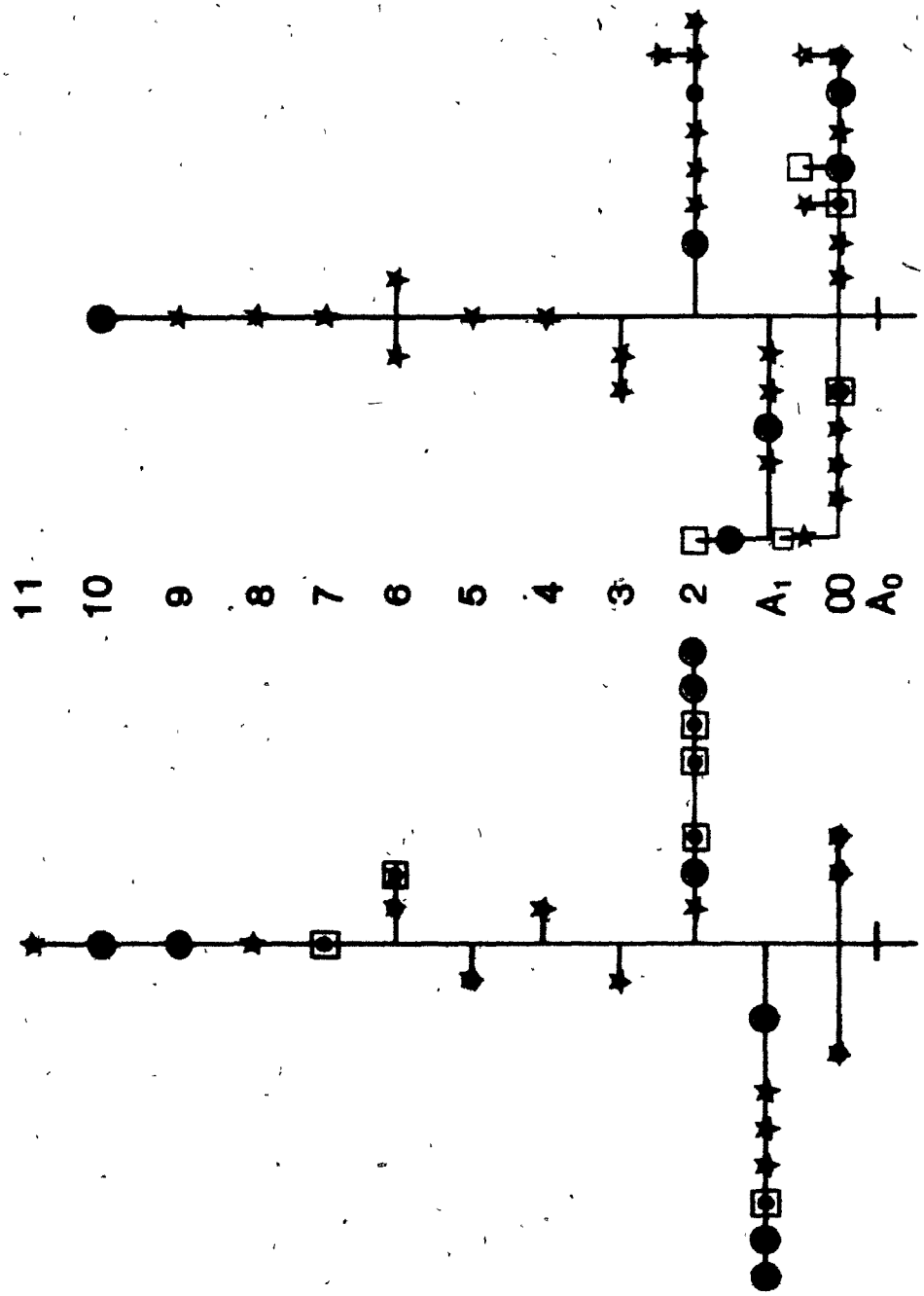
Detailed observation throughout the experimental period allowed for the 'mapping' of peduncle activity for this cultivar (Figure 3). Though the two replicates were different in some respects, the overall picture

Figure 3

Diagrammatic representation of cowpea cv. Vita-5:

an explanatory key

Ao	=	cotyledonary node
OO	=	simple opposite leaves
A1-An	=	main stem node number
——	=	side branch arising from main stem node
|	=	vegetative node
●	=	peduncle appearing during the 'flush' of those which contribute to yield
●	=	as for (●) but which undergo reproductive activity
●	=	as for (●) but which remain reproductive and contribute to yield
✯	=	peduncles becoming active in the few days preceding harvest (that is, during seed desiccation)
□	=	peduncles which abscise


11
10
9
8
7
6
5
4
3
2
A1
A0

is similar. Peduncle activity for the majority of peduncle sites appears to have been arrested (that is, the peduncles ceased to elongate), suppressed (that is, peduncles came into activity only when active sites had ceased maturing), or ceased (that is, abscission), while relatively few peduncles became and remained reproductive.

In both instances, the plants had developed a large number of vegetative nodes which failed to have an associated peduncle which contributed to yield (83% average). Though it might be assumed that the vegetative structure was required to obtain this yield level, it was observed that the plants were not senescent at harvest, suggesting that not all mobilized and current assimilates were used for yield accretion.

With the plants laid out in two dimensions as in the diagram, another feature is also apparent. The lower third of the plant (that is, node 3 and below, including branches) was responsible for contributing the majority of the peduncles which contributed to yield. When translated into terms of actual yield, the bottom, middle, and top thirds represented accumulations of 80, 0, and 20%, respectively. This is presented in Figure 4 along with similar observations for the other cultivars screened. It can be seen that for this cultivar, and indeed for a good number of the other cultivars, that the lower third of the plant accumulated a high proportion of the yield. The findings varied considerably among cultivars, and though very few of the cultivars expressed this characteristic as strongly as Vita-5, the bottom thirds of the majority of the cultivars were shown to be responsible for over 60% of the yield accumulated.

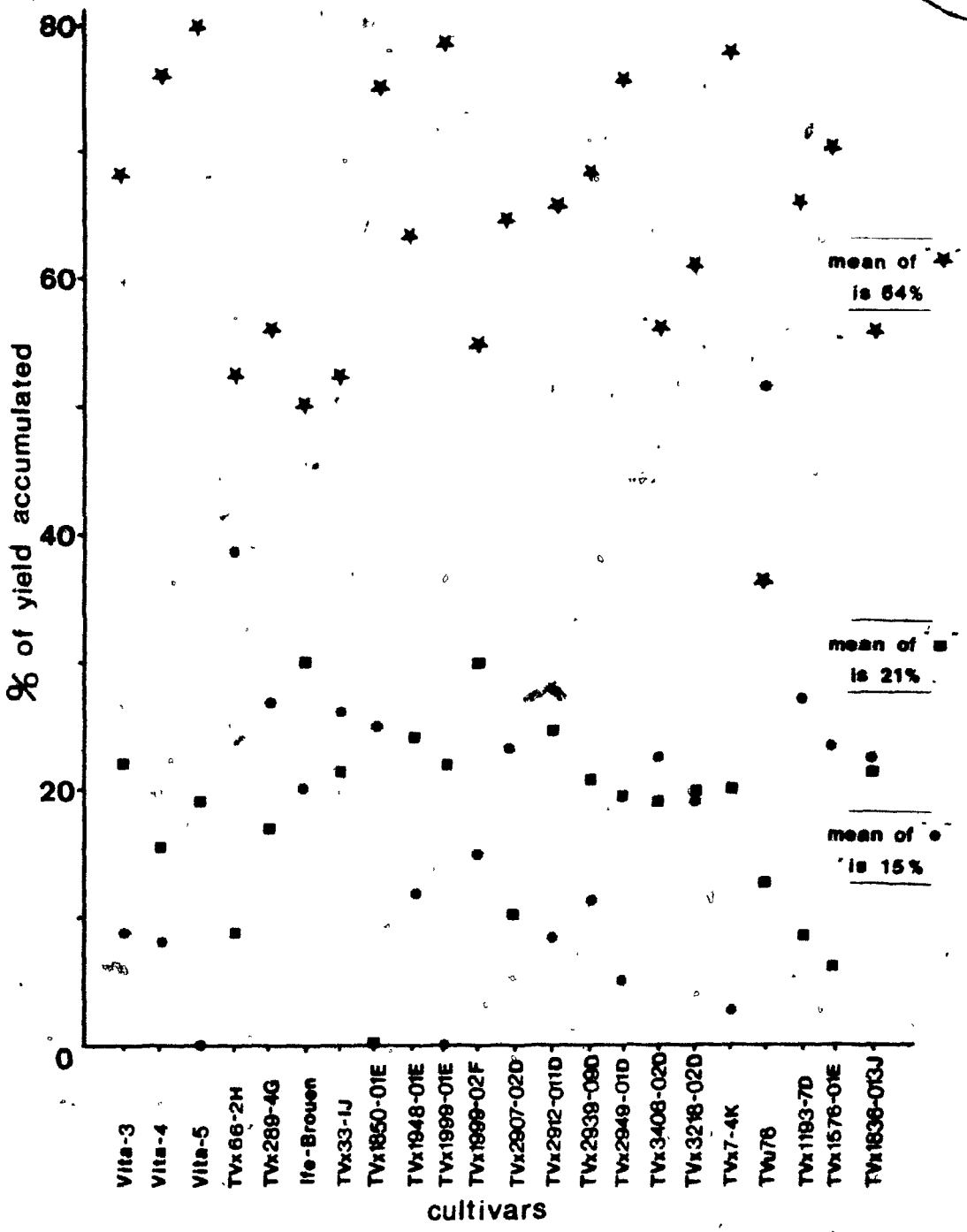
Figure 4

Percent of yield accumulated by the top, middle, and bottom thirds of plants for twenty-two cultivars of cowpea (Vigna unguiculata (L.) Walp.) (means of two replicates)

● = top third

▬ = middle third

★ = bottom third


80
60
40
20
0
% of yield accumulated
mean of ★ is 64%
mean of ■ is 21%
mean of ● is 15%
Vita-3
Vita-4
Vita-5
TVx 66-2H
TVx 289-4G
Ife-Brown
TVx 33-1J
TVx 1850-01E
TVx 1948-01E
TVx 1999-01E
TVx 1999-02F
TVx 2907-02D
TVx 2912-01D
TVx 2939-08D
TVx 2949-01D
TVx 3408-02D
TVx 3218-02D
TVx 7-4K
TVu 76
TVx 1193-7D
TVx 1576-01E
TVx 1836-013J
cultivars

When averaged over all the varieties examined, the bottom, middle, and top thirds were found to contribute yield proportions in the order of 64, 15, and 21 %, respectively. The author suggests that for many cultivars, and Vita-5 in particular, the activities of the upper main stem may interfere with the reproductive productivity of the lower stem nodes, while contributing fairly little to yield.

2.4 Conclusions

Based on the findings of this screening, the cultivar Vita-5, showing a very high level of peduncle inactivity, was selected for further study.

In this variety, it was observed that relatively little yield was contibuted by the upper two thirds of the plant, despite the presence of several potential sites. This observation was quantified for all the varieties tested and was observed to be true for the majority of these cultivars. It was suggested that the activities of the main stem may have limited the reproductive productivity of the lower stem node branches. It was also observed that a large number of peduncles appeared to be inactive due to the activities of relatively few.

Based on these findings, two lines of research were chosen to be conducted using cv. Vita-5:

(1) To establish the role of branching and apical dominance in yield accretion (Experimental Series I. Section 3).

(2) To establish a model (non-mathematical) for 'intra-sink' competition between peduncle sites (Experimental Series II. Section 4).

3. EXPERIMENT SERIES I. A POSSIBLE ROLE FOR APICAL DOMINANCE AND BRANCHING IN YIELD ACCRETION BY COWPEA

3.1 Introduction

3.1.1 Apical dominance A characteristic feature of plant development is that more apical shoot meristems are initiated than fully develop. Of these, the apical bud meristem generally grows much more vigorously than the lateral, often axillary, bud meristems. Notwithstanding variations according to age, species (Phillips, 1975), nutritional status (Gregory and Veale, 1957; Woolley and Wareing, 1972), light intensity (Woolley and Wareing, op. cit.; Phillips, 1969), and photoperiod (Phillips, op. cit.), it is feasible to say that all axillary buds are subject to inhibition by the apical bud. This inhibition of lateral buds is referred to as apical dominance and is released by decapitation (Thimann and Skoog, 1933).

The Drosophila of fundamental plant physiology, legumes have been used in a multitude of experiments relating to apical dominance (among many others, Shein and Jackson, 1971; Everat-Bourbouloux and Charnay, 1982; Van Staden and Carmi, 1982). Similarly, in grain legume species, decapitation has been performed at different stages of growth in order to simulate hail injury, insect predation, or to define the spatio-temporal effects on branching and yield: cowpea (Ezedinma, 1973a; Stewart, 1976), pigeon pea (Tayo, 1982), and soybean (Greer and Anderson 1965; Bauer et al., 1976; Tayo, 1980). Depending on the stage of growth and several other factors, various yield responses (inhibitory,

stimulatory, or neutral) were reported; but in all of these studies , decapitation resulted in the stimulation of branching.

Although early investigators of apical dominance phenomena emphasized the importance of nutrients and water supply in the regulation of lateral bud development (Gregory and Veale, 1957), considerable evidence has mounted against the view that nutrient availability and supply underly this mechanism (Goodwin and Cansfield, 1967). Though nutrient status in the plant is probably involved, the correlative signal would appear to have a primarily hormonal basis.

3.1.2 Hormone involvement in, and growth regulation of apical dominance

Soon after the discovery that auxin was synthesized in growing apical buds, Thimann and Skoog (1933,1934) reported that exogenous IAA (indole-3 acetic acid) could substitute for the apical bud in maintaining axillary bud inhibition in bean plants. All classes of phytohormones have since been implicated as having a role in or an influence on apical dominance or lateral bud outgrowth; though for some these functions have not as yet been firmly established (Wickson and Thimann, 1958; Catalino and Hill, 1969; Phillips, 1971; Yeang and Hillman, 1982). A significant discovery in this respect has been the observation that direct applications of synthetic cytokinins to inhibited buds of a number of species can elicit their outgrowth (Wickson and Thimann, 1958; Sachs and Thimann, 1964, 1967).

Exploitation of this response has been investigated for a number of horticultural species, in which the stimulation of lateral bud

development can represent a major input. With several floricultural species, for example, the current practice for producing potted plants involves the pinching and removal of terminal buds in order to induce branching, both to improve the shape of the plant and to increase the number of flowers produced (Jeffcoat, 1977). Foliar applications of the synthetic cytokinins BA (6-benzyl aminopurine) and PBA (6-benzyl amino-9-(tetrahydropyran-2-yl)- 9H-purine) have been reported to stimulate branching in a number of ornamental crops including: Rhododendron spp. (azalea) (Jackson and Dingle,1971); Dianthus spp. (carnation) (Jackson, 1975; Jeffcoat, 1977); Chrysanthemum spp.(chrysanthemum) (Carpenter and Carlson, 1972; Jeffcoat, 1977); Pelargonium hortorum (geranium)(Carpenter et al., 1972); Photinia spp. (photinia) (Ryan, 1974), Euphorbia pulcherima Willd. (pointsettia) (Jeffcoat, 1977), and Rosa spp. (rose) (Carpenter and Rodriguez, 1971; Faber and White, 1977; Ohkawa,1979). Many studies, that of Acati et. al. (1980) among others, reveal that several cytokinins, if applied optimally, will successfully replace the handpinching of floricultural crops and may, in fact, stimulate the growth of lateral buds, and consequently flowering sites, which would not generally develop after handpinching.

Other growth-regulating chemicals which are not synthetic hormones are thought to or known to interfere with apical dominance. The effects of TIBA (2,3,5 - triiodobenzoic acid) on partial loss of apical dominance in soybeans was first noted by Galston (1947). Several other observers have further substantiated this claim (Hicks et. al., 1967; Bauer et. al., 1969) and the mode of action has since been better

qualified. Several researchers have demonstrated that TIBA acts as an inhibitor to IAA transport within the plant (Hay,1956; Niedergang-Kamien and Skoog, 1956; Zwar and Rijven, 1956; Niedergang-Kamien and Leopold, 1957). When auxin movement from the terminal bud on a shoot is blocked, the lateral buds are thought to be released from inhibition and grow out into side shoots. The application of TIBA has been found to stimulate grain yields for a number of grain legume species: chickpea (Sinha and Ghildiyal, 1973); cowpea (Hipp and Cowley, 1969); pigeon pea (Reddy and Zaheda, 1979); soybean (Bauer et. al.,1969; Clapp, 1973); though the afore-mentioned changes in crop morphology may not have been responsible.

3.1.3 Objectives This series of experiments was undertaken to determine the role that apical dominance and branching might play in yield accretion by cowpea, using chemical and manipulative treatments known or thought to be involved in releasing axillary buds from inhibition.

3.2 Materials and Methods

This section describes the materials and methods which were common to many or all of the experiments which were conducted in this series, in order to avoid undue repetition.

3.2.1 Experiments conducted in standard glasshouses For all experiments conducted in the standard glasshouses, techniques as well as the site were identical to those of the cultivar screening (Section 2.2).

3.2.2 Experiments conducted in controlled environment growth cabinets

As in the glasshouse experiments, the plants were maintained in an environment simulating the site of their selection, except that these facilities permitted more effective standardization of environmental variables. The plants were grown using many of the husbandry and management guidelines previously described for the growing of this species under simulated tropical condtions in controlled environments (Huxley and Summerfield, 1976; Summerfield et al., 1977).

3.2.2.1 Growth cabinets and environmental controls The growth cabinets (Sherer Controlled EnvironmentLab model CEL37-14: 1.85m x 0.85m floor area; 2.0m high) allowed precise control of daylength, and day

and night temperatures. All plants were hence grown at the mean values of daylength, and meteorological screen day and night temperatures of the main growing season at Ibadan, Nigeria (from Huxley and Summerfield, 1976). They were supplied with a twelve hour thirty minute photoperiod and a day/night temperature regime of 30°C/21°C. Plants received 285 microeinsteins/ m^2/ sec radiation supplied by 'cool-white' fluorescent bulbs (manufactured by General Electric Inc.) with tungsten bulbs contributing approximately fourteen percent of the total rated output wattage per cabinet.

3.2.2.2 Plant husbandry All plants were grown in 18-cm diameter plastic pots containing a drainage layer of clay chips and a John Innes Potting Compost no. 1 (Bunt, 1976), which was modified from earlier experiments in order to reduce organic constituents and enhance drainage, after difficulties with fungus gnats (Sciarria spp.) were encountered. Hence, in all cabinet experiments, pre-plant incorporated slow release organic fertilizers were replaced by manufacturer's recommendations of Osmocote 14-14-14, and turfite replaced one half of the sand requirement.

All other techniques were identical to those of the glasshouse experiments except that the isolated conditions of the cabinets did not require pest control, since the facilities were well scrubbed (with soap solutions followed by 5% chlorine solutions and rinsings) prior to use.

3.2.3 Plant growth regulator use: Selection of concentrations The choice of concentrations for the plant growth regulators was based on scrutiny of favorable responses observed by other researchers. For TIBA, such responses have been observed for concentrations ranging from 10 to 300 ppm : broad bean (Newaz and Lawes, 1980); chickpea (Sinha and Ghildiyal, 1973); cowpea (Hipp and Cowley,1969); pigeon pea (Reddy and Zaheda, 1979); soybean (Galston, 1947; Greer and Anderson, 1965; Burton and Curley, 1966; Wax and Pendleton, 1968; Sant'Anna et al., 1970; Basnet et al., 1972; Clapp, 1973; Chowdhury et al., 1978). For cowpea in particular, a favorable response has been observed with concentrations of about 60-70 ppm (Hipp and Cowley, 1969). For the pilot study, concentrations of 50, 100, and 200 ppm were used.

In the case of benzyladenine, no works of particular significance to grain legumes in general, and cowpea in particular, were found by the author. Studies with foliar sprays on floricultural species were hence used as a guideline. In such studies, favorable responses of branching and flower yields have been observed with concentrations ranging from 400 ppm to 1000 ppm: chrysanthemum (Carpenter and Carlson, 1972); geranium (Carpenter et al.,1972); pointsettia (Carpenter et al., 1971). For the pilot study, concentrations of 250, 500, and 1000 ppm were selected.

3.2.4 Solution preparation and application Preliminary assays on the solubility of the plant growth regulators were conducted in order to determine the lowest quantity of solvent required, prior to dilution

of these with water for use as foliar sprays. The solvents used were determined by previous findings for TIBA (Greer and Anderson, 1965) and by solubility information obtained from the Merck Index (Stecher, 1968) for BA. Solutions of TIBA were formulated by dissolving 1 g of the compound in 30 ml of 95% ethanol, while those of BA were obtained by dissolving 1 g in 20 ml of 0.5M NaOH. Stock solutions were obtained by further dissolving these solutions with water up to 1 litre and 500 ml , respectively. For TIBA stock solutions, the bottles were kept completely covered with aluminum foil in order to alleviate light degradation (Greer and Anderson, 1965).

For applications of both plant growth regulators to the plants, proper volumes of the stock solutions were diluted to the desired concentrations with water containing 0.05% Tween 20 (polyoxyethylene sorbitan monolaurate) as a surfactant. Plants were sprayed to the point of runoff using hand held atomizers.

Two types of control - one 'dry' and the other, sprayed with a solvent/0.05% surfactant solution, 'wet', were run in order to ascertain possible effects due to the solvents and the surfactant.

3.2.5 Timing of treatments The timing of growth regulator applications and decapitation treatments was also based on scrutiny of the literature. Though favorable responses have been observed for TIBA applications to a number of crops at several stages of growth, the majority of studies point to early flowering as being the most favorable, or at least among the most favorable: chickpea (Sinha and

Ghildiyal, 1973); cowpea (Hipp and Cowley, 1969); pigeon pea (Reddy and Zaheda, 1979); soybean (Greer and Anderson, 1965; Burton and Curley, 1966; Wax and Pendleton, 1968; Bauer et al., 1969; Campbell and Greig,1974). Consequently, all TIBA applications referred to in this series were applied at this stage of growth.

Decapitation was performed during vegetative growth since most favorable responses have arisen after decapitation during these stages or during early bloom : cowpea (Ezedinma, 1973a; Stewart, 1976); pigeon pea (Tayo, 1982); and soybean (Tayo, 1980). For cowpea in particular, Stewart (1976) reported increases for many yield components and total yields for decapitation conducted between the fourth and fifth nodes of the main stem. This stage of growth was chosen for the present study and decapitation was effected by a single cut using a sharp scalpel at full expansion of the trifoliate leaf at the fifth node.

Benzyladenine solutions were also applied at this stage of growth since they have been shown to be similar in action to decapitation (or pinching) in the studies cited previously for floricultural species.

3.2.6. Statistical analysis Analyses of variance were performed on all variables for these experiments and comparisons of means were performed using the Duncan's new multiple range test or the least significant difference (l.s.d) test when the analysis of variance indicated significant differences for a given variable.

3.3 Experiment 1. Pilot study to determine the effects of various concentrations of TIBA on yield components of cowpea cv. Vita-5

3.3.1 Objectives In the summer of 1981, a greenhouse pilot study was conducted in order to determine the effects of various concentrations of TIBA on the yield components of cowpea cv. Vita-5 and to establish a concentration with a favorable response of interest for further study.

3.3.2 Materials and methods The materials and methodology used were as described in Section 3.2, using TIBA concentrations of 50, 100, and 200 ppm. As described, both a 'wet' and a 'dry' control were included.

All treatments were replicated three times and laid out in a randomized complete block design, blocked against a suspected north-south light gradient. Yield data was taken at harvest.

3.3.3 Results Results are presented in Figure 5 and Appendices B1.1 and B1.2. For the majority of yield components (except for the number of pods per plant), no significant differences were observed between 'wet' and 'dry' controls, suggesting no effect due to the solvent or surfactant. If at all, these effects were stimulatory.

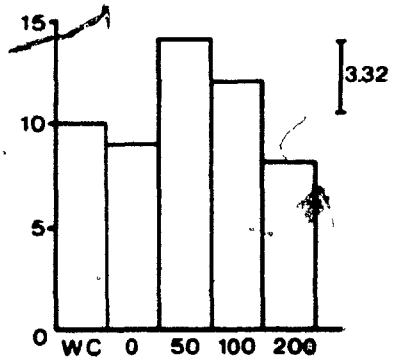
Figure 5

Yield components of cowpea cv. Vita-5 at various concentrations of TIBA (means of three replicates)

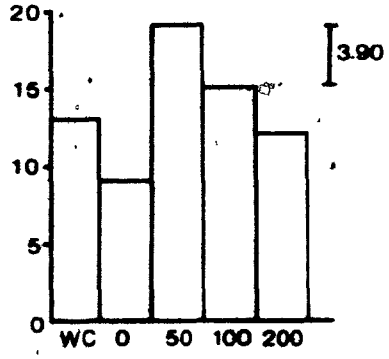
WC	Wet control (ethanol/ Tween 20/ water solution)
0	Dry control
50	50 ppm TIBA (in Tween 20/ water solution)
100	100 ppm TIBA (in Tween 20/ water solution)
200	200 ppm TIBA (in Tween 20/ water solution)

 = L.S.D. of pairs of treatments at alpha = 0.05

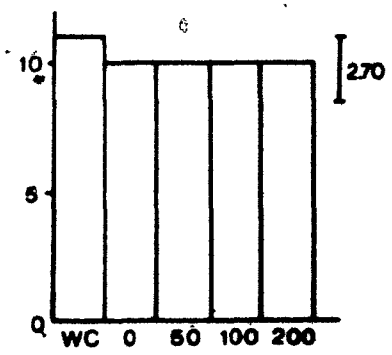
a) NUMBER OF ACTIVE PEDUNCLES PLANT^{-1}



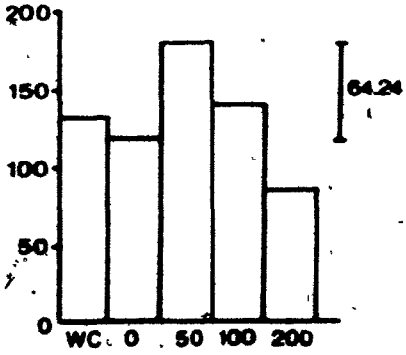
b) NUMBER OF PODS PLANT^{-1}



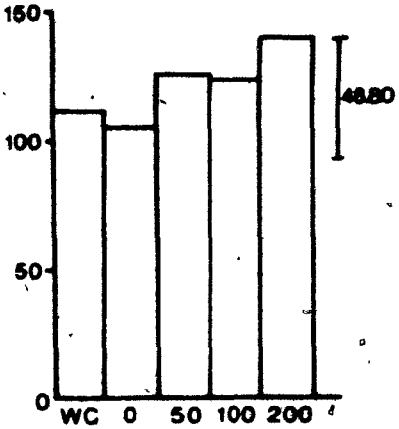
c) NUMBER OF SEEDS POD^{-1}



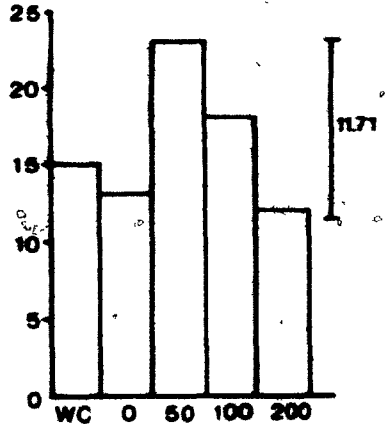
d) NUMBER OF SEEDS PLANT^{-1}



e) MEAN SEED WEIGHT (mg)



f) TOTAL SEED YIELD (g) PLANT^{-1}



TIBA, at the lowest concentration, enhanced all the yield components recorded, excluding the number of seeds per pod, which was fairly uniform over all treatments. The number of active peduncles per plant - a primary yield component representing the number of peduncles contributing to yield - was 36% higher for the 50 ppm TIBA treatment than for the dry control. The effect of this enhancement of the primary yield component was reflected in increased pods per plant, seeds per plant, and total seed yields (with significant correlations of p = +0.90, +0.65, and +0.63, respectively) (Appendix B1.2). A 25% increase in the number of active peduncles was observed for the intermediate concentration of TIBA (100 ppm), though neither this concentration nor the highest (200 ppm) was found to have a significant effect on this yield component.

This effect was fairly consistent over the other yield components for which significant differences between treatments were observed (number of pods per plant, number of seeds per pod, and total seed yield in grams). For the number of seeds per plant, though the 50 ppm TIBA treatment yielded approximately 30% more seeds than that of the controls, significant differences were observed only between the 50 ppm and 200 ppm TIBA treatments, which produced 182 and 86 seeds, respectively. The mean seed weight for this latter concentration was somewhat higher than that of the lower concentration, however.

Differences in total seed yields (expressed as grams per plant) were a direct reflection of differences in the other yield components, with significant correlations with the number of peduncles per plant, pods per plant, seeds per plant, and seeds per pod (p = +0.63, +0.77, +0.90,

and +0.58, respectively) (Appendix B1.2). Total seed yields were increased 44% by applications of 50 ppm TIBA, though this was not found to be statistically significant.

3.4 Experiment 2. The effects of TIBA on the growth and yield of cowpea cv. Vita-5

3.4.1 Objectives In the autumn of 1981, a detailed controlled environment study was conducted in order to determine the effects of TIBA on the growth and yield of cowpea cv. Vita-5 in order to clarify understanding of the yield increases observed in the pilot study.

3.4.2 Materials and methods This controlled environment study was performed using the materials and methods described in Section 3.2. Based on the results of the pilot study, a 50 ppm concentration of TIBA was used and a wet control was excluded. Treated plants were hence compared to dry controls and the two treatments were each performed on four plants distributed throughout the cabinet in a completely randomized design. Plant positions were randomly rotated within the cabinet on a daily basis when readings were taken. Both vegetative and reproductive yield data were taken at harvest, the dry matter yields for aerial vegetative material being weighed after drying of the plants for 30 hours at 60°C in a forced hot air dryer. Yield data were taken at harvest.

3.4.3 Results Results of this experiment are presented in Tables 4 and 5 and Appendix B2. Unlike the case for the pilot study, a 50 ppm

Table 4. Yield components of cowpea cv. Vita-5 treated with TIBA at first flowering

TIBA concentration (ppm)	Number active peduncles plant^{-1}	Number pods plant^{-1}	Number seeds pod^{-1}	Number seeds plant^{-1}	Mean seed weight (mg)	Seed weight plant^{-1} (g)
0	3.00 a	3.25 a	7.58 a	22.50 b	149.56 a	3.34 a
50	4.75 a	5.00 a	7.48 a	31.75 a	119.20 b	3.75 a

Figures represent the means of four observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05.

concentration of TIBA applied to the leaves of plants grown in this controlled environment had very few significant effects on yield components (Table 4). Though peduncle and pod numbers were increased approximately 35% each by the treatment, these effects did not reach significant levels. Seed numbers were increased by TIBA treatment, however, but the possible compensatory influence of lower mean seed weights resulted in total seed yields similar to those of the control plants. It is important to note that the yields of this growth cabinet study were notably less than those of the greenhouse pilot study, and that the less marked differences might be a reflection of a lower vigor of growth, and, consequently, a less dynamic yielding situation.

Table 5. Vegetative attributes of cowpea cv. Vita-5 for TIBA applied at first flowering.

TIBA concentration (ppm)	Number branches plant^{-1}	Number nodes plant^{-1}	Number nodes from branches plant^{-1}	Number main stem nodes plant^{-1}	Aerial vegetative dry weight (g)	Mean internode length (cm)
0	5.00 a	17.00 a	4.00 a	11.75 a	14.3 a	6.79 b
50	5.00 a	15.25 a	6.25 a	12.50 a	14.1 a	4.73 a

Figures represent the means of four observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05.

In this study, TIBA had no notable effects on branching and other vegetative components (Table 5). Branch number was entirely unaffected, and the number of nodes which arose from these branches was not affected. Overall, the number of nodes resulting from the treatment was nearly identical to that of the control plants , and this was further reflected in the aerial vegetative dry weight which was accumulated. The only significant difference observed was in the lengths of the internodes of the main stem, which were 30% shorter for TIBA-treated plants. This allowed for a greater number of main stem nodes (12.5 versus 11.75) over a shorter overall height (69 versus 75 cm), as reflected in Plate 2.

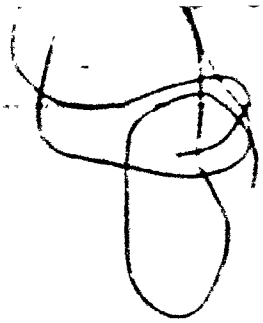


Plate 2

Untreated plant and TIBA treated plant prior to harvest

3.5 Experiment 3. Pilot study to determine the effects of various concentrations of 6-benzyladenine on yield components of cowpea cv. Vita-5

3.5.1 Objectives In the summer of 1982, a greenhouse pilot study was conducted in order to determine the effects of various concentrations and two modes of application of 6-benzyladenine on the yield components of cowpea cv. Vita-5 and to establish a concentration with a favorable response, of interest for further study.

3.5.2 Materials and methods The materials and methodology used here were those described in Section 3.2. The experiment was conducted as a factorial with two modes of application (foliar spray and axillary bud brush) and three concentrations of 6-benzyladenine (100, 250, and 1000 ppm). The foliar sprays were applied at full expansion of the fifth leaf on the main stem, as described in Section 3.2.3. The axillary bud brush applications were performed at this same stage of growth, but involved the application of 100 microliter droplets of the benzyladenine solutions to all axillary buds. These droplets were spread over the buds with a fine artist's paintbrush. Based on the lack of significant differences between 'wet' and 'dry' controls for the TIBA pilot study, only dry controls were included in this study.

All treatments were replicated three times and laid out in a

randomized complete block design against a suspected north-south light gradient. Yield data were taken at harvest.

3.5.3 Results Results are presented in table 6 and Appendix B3. No significant differences were observed between the two modes of benzyladenine application; nor were there significant interactions between the two factors (concentration and mode of application) under study (Appendix B3). Averaged over both application types, no statistically significant differences were found between 6-benzyladenine (BA) concentrations for any of the variables under study (Table 6). Trends were nonetheless observed. BA applications at the highest concentration (1000 ppm) increased the majority of yield components. For this treatment, two more peduncles became and remained productive, and 36% more pods were produced than those of the control plants. While the same number of seeds per pod as the controls were produced for this treatment, the greater number of seeds resulting from a greater number of pods was reflected in a 33% increase in total seed yield. In comparison to the control plants some yield enhancement was observed for the other benzyladenine concentration treatments and this was due to increases in either the number of pods produced (250 ppm) or the number of seeds per pod (100 ppm). The increases in total seed yield were not as marked as that arising from the 1000 ppm treatments, however.

Table 6. Yield components of cowpea cv. Vita-5 treated with 6-benzyladenine at the 5-leaf stage (averaged over two modes of application).

Benzyladenine concentration (ppm)	Number active peduncles plant^{-1}	Number pods plant^{-1}	Number seeds pod^{-1}	Number seeds plant^{-1}	Mean seed weight	Seed weight plant^{-1}
0	4.83	7.00	8.44	60.17	147.83	8.59
100	4.67	7.17	10.11	71.33	145.13	10.37
250	6.17	9.17	7.09	64.33	144.63	9.36
1000	7.33	11.00	7.80	84.17	143.70	11.96

Figures represent the means of six observations.

3.6 Experiment 4. The effects of decapitation and 6-benzyladenine treatments on the growth and yield of cowpea cv. Vita-5

3.6.1 Objectives In the autumn of 1982, a detailed controlled environment study was conducted in order to determine the effects of various decapitation and 6-benzyladenine treatments on the growth and yields of cowpea cv. Vita-5.

3.6.2 Materials and methods This controlled environment study was performed using the materials and methods described in Section 3.2. Based on the pilot study, 1000 ppm concentrations of BA were used. A completely randomized design comprising five treatments with four replicates for each treatment was employed:

(a) Control - no decapitation or benzyladenine;

(b) Plants decapitated between the fourth and fifth node of the main stem at full expansion of the trifoliate leaf at the fifth node;

(c) Plants decapitated as in (b) with 100 microliter droplets of the 1000 ppm benzyladenine solution brushed on to all axillary buds present at this time;

(d) Plants treated at the same stage of growth as (b) with a foliar spray of the 1000 ppm benzyladenine solution applied to the point of run-off;

(e) Plants decapitated as in (b) and treated with a foliar spray as in (d).

Plant ontogeny and harvest data were recorded as in the TIBA study (Section 3.4).

3.6.3 Results Results for this experiment are reported in Tables 7, 8, and 9; Figure 6; and Appendices B4.1, B4.2, and B4.3. The various treatments had no statistically significant effect on the number of branches per se (Table 7). The number of nodes originating from these branches, and consequently the number of nodes per branch, was affected however. In all cases, decapitation treatments increased the number of nodes which arose from these branches, the greatest increases occuring when benzyladenine was brushed on to the axillary buds in combination. In this case, the number of nodes originating from the branches was nearly three-fold that of the untreated plants. The spraying of BA resulted in no such increase, however, unless this was combined with decapitation. This stimulation of branching components was similarly reflected in the number of nodes initiated per branch. Decapitation and decapitation/benzyladenine treatment combinations increased this component two to three-fold, while benzyladenine had no effect unless combined with decapitation.

The treatments had no statistically significant effects on either the number of peduncles which became and remained reproductive or on the number of pods which reached maturity (Table 8). Despite this, some differences were observed and all treatments resulted in slight

increases in pod yields over those of the control plants. Significant differences were noted for seed number, however. Decapitation alone resulted in a 68% increase in the number of seeds while use of a

Table 7. Yield components of cowpea cv. Vita-5 for various decapitation and 6-benzyladenine treaments.

Treatment	Number branches plant^{-1}	Number nodes originating from branches plant^{-1}	Number nodes per branch plant^{-1}
1. Control	4.00 a	4.00 c	1.00 c
2. Decapitation	4.50 a	12.50 ab	2.94 a
3. Decapitation + BA (brush)	5.00 a	15.00 a	3.04 a
4. BA (spray)	2.75 a	3.00 c	1.05 c
5. Decapitation + BA (spray)	4.75 a	10.25 b	2.17 b

Figures represent the means of four observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05.

benzyladenine spray decreased the number of seeds - though only slightly. Axillary bud treatment with benzyladenine following decapitation had no effect on the seed number. Differences here were no doubt a reflection of the number of seeds per pod, which followed a similar trend. The mean seed weight remained unaffected by the treatments.

Table 8. Yield components of cowpea cv. Vita-5 for various decapitation and 6-benzyladenine treatments.

Treatment	Number active peduncles plant^{-1}	Number pods plant^{-1}	Number seeds pod^{-1}	Number seeds plant^{-1}	Mean seed weight (mg)	Seed weight plant (g)
1. Control	3.00 a	3.25 a	7.58 ab	22.50 ab	149.56 a	3.34 c
2. Decapitation	3.00 a	4.50 a	8.73 a	38.00 a	132.98 a	5.06 a
3. Decapitation + BA (brush)	3.75 a	5.25 a	5.56 bc	26.75 ab	151.41 a	4.04 b
4. BA (spray)	3.00 a	5.50 a	3.79 c	20.75 c	154.82 a	3.18 c
5. Decapitation + BA (spray)	4.25 a	5.25 a	4.24 a	21.50 c	149.61 a	3.21 c

Figures represent the means of four observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05.

Differences in total seed yields were also observed to be a reflection of variations in the number of seeds per pod and seed numbers, with significant correlations of p=+0.49 and p=+0.93, respectively (Appendix B4.2). Highest total yields in grams were observed for decapitation alone, which resulted in a yield increment of 51% over that of the control plants. In the treatment in which benzyladenine was applied to axillary buds following decapitation, a total yield increase of 21% was observed, while neither of the treatments in which benzyladenine was sprayed on the leaves had a significant effect on total seed yield.

Other, more striking observations were made with regard to treatment effects on vegetative components and harvest indices (Figure 6). The control plants yielded greater aerial dry weights than those of any of the treatments (Figure 6b), and this was no doubt a direct reflection of the accumulation of a greater amount of vegetative dry matter (leaves and stems, Figure 6a), with which total dry matter yields were signifcantly correlated (p=+0.97) (Appendix B4.3). Where axillary buds were treated with benzyladenine following decapitation, no significant differences from the control were observed, however. Decapitation alone decreased vegetative matter significantly however, and this effect was even more pronounced when combined with foliar spray applications of benzyladenine. Both treatments involving this mode of benzyladenine application yielded significantly lower quantities of vegetative dry matter than any other treatment (both approximately 50% lower than that of the control plants). The effect of the foliar spray appeared to have been independent of whether or not the plants had been decapitated, as there were no significant differences between these two treatments.

Accumulation of vegetative dry matter appears to have been a reflection of the total number of nodes (and consequently, leaves) present at the end of the experiment (Figure 6c), and this variable was highly associated with the former (p=+0.72) (Appendix B4.3). This in turn was a reflection of the number of nodes apppearing after treatment, with which the total number of nodes was significantly correlated (p=+0.95). Decapitation alone had no significant effect on these two components, while decapitation plus application of benzyladenine to the

Figure 6

Vegetative and yield attributes of cowpea cv. Vita 5 for a number of decapitation and benzyladenine treatments (means of 4 replicates)

C - Dry control

D - Decapitation between the fourth and fifth nodes at expansion of the fifth true leaf

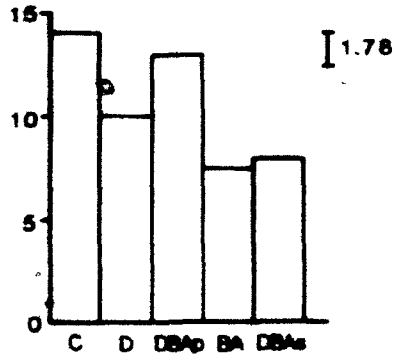
DBAp - As for 'D' but with a 1000 ppm 6-benzyladenine solution applied to all axillary buds

BA - Application of a 1000 ppm 6-benzyladenine spray to plants at the same stage of growth as 'D'

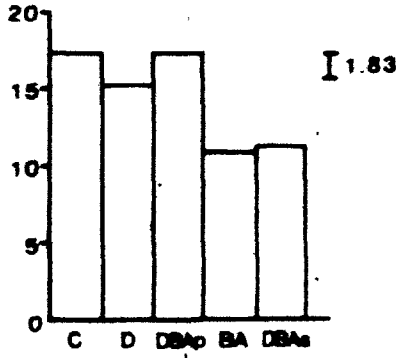
DBAs - As for 'D' combined with the foliar spray of 'BA'

I - L.S.D. of pairs of treatments at alpha = 0.05

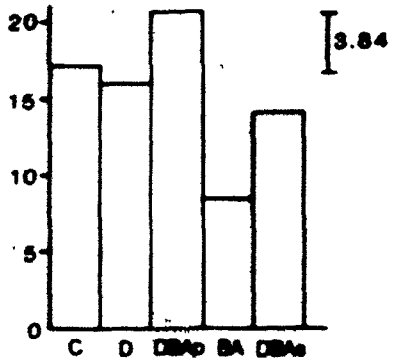
a) AERIAL VEGETATIVE DRY WEIGHT (g) PER PLANT



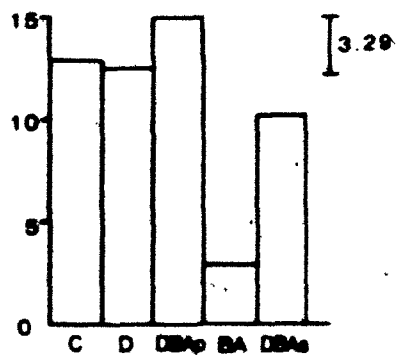
b) TOTAL AERIAL DRY WEIGHT (g) PER PLANT



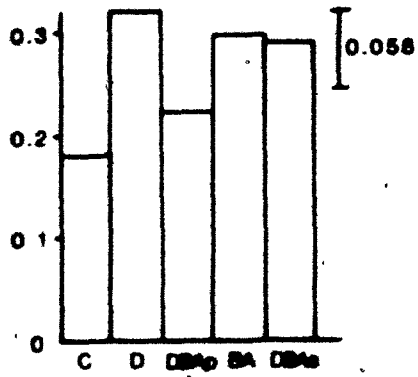
c) FINAL NODE NUMBER PER PLANT



d) NUMBER OF NODES APPEARING AFTER TREATMENT PER PLANT



e) HARVEST INDEX



axillary buds had a stimulatory effect on the total number of nodes. This was undoubtedly a reflection of the number of nodes which appeared after treatment, and though no statistically significant difference was observed, 15% more nodes than those of the controls appeared after treatments. Foliar applications of benzyladenine without decapitation significantly inhibited (72%) the number of nodes appearing after treatment, while this treatment in combination with decapitation had an intermediate effect.

The effects of the various treatments on the harvest indices (a measure of yield efficiency, H.I. = grain yield/biological yield (grain yield plus vegetative yield)) were negatively correlated with the effects on vegetative dry matter accretion ($p=-0.76$) (Appendix B4.3). All treatments (except for decapitation combined with benzyladenine application to axillary buds) yielded harvest indices greater than those of the control plants (Figure 6e). For the latter treatment, the lower harvest index was surely a reflection of greater dry matter accretion (Figure 6a).

The observations presented here are clearly visible when viewed pictorially (Plate 3). It is evident from the picture that some treatments had notable effects on vegetative components. Decapitation alone can be seen to have had very little effect on the overall plant structure, with one branch taking over the lead of the main apex. Such was the case for the plants which had benzyladenine applied to the axillary buds following decapitation. In this case, however, the lower nodes were more strongly branched and the general growth was in excess of that of both the control plant and the plant which was only

Plate 3

Plants of various decapitation and benzyladenine treatments at harvest:

an explanatory key

CONTROL	-	untreated
DECAP	-	plants decapitated between the fourth and fifth main stem nodes at full expansion of the trifoliate leaf at the fifth node
DECAP-BA(B)	-	plants decapitated as in 'DECAP' with 100 microliter droplets of a 1000 ppm BA solution brushed on to all axillary buds present at this time.
BA SPRAY	-	plants treated at the same stage of growth as 'DECAP' with a foliar spray of a 1000 ppm BA solution applied to the point of run-off
DECAP-BA(S)	-	plants decapitated as in 'DECAP' and also treated with a foliar spray as in 'BA SPRAY'

decapitated.

The plants which were visibly most different from the control plants were those which received foliar benzyladenine sprays, both with and without decapitation. In both cases, the vegetative growth was strikingly less abundant than that of the controls. In addition, height was significantly affected by such treatment (Table 9). A benzyladenine spray without decapitation decreased height by 47% with respect to the control plants, while this treatment in combination

Table 9. Height and mean internode length of main axis of cowpea cv. Vita-5 for various decapitation and 6-benzyladenine treatments.

Treatment	Height (cm)	Mean main axis internode length (cm)*
1. Control	75.00 a	6.77 a
2. Decapitation	75.00 a	-
3. Decapitation + BA (brush)	72.50 a	-
4. BA (spray)	39.50 b	1.95 b
5. Decapitation + BA (spray)	33.00 b	-

* Not feasible to study on decapitated plants as main stem activities were curtailed by treatment
Figures represent the means of six observations.
Duncan's new multiple range test.
Within columns, means with the same letter are not significantly different at alpha=0.05.

with decapitation lowered plant heights further still (56% less than both control plants and plants which were only decapitated). Part of this was no doubt due to a decrease in internode length (Table 9). The mean internode length for plants receivng a benzyladenine spray was 71% less than that of the control plants.

3.7 Discussion

The apical bud is known to exert dominance on growth of the shoot normally resulting in the suppression of lateral bud outgrowth. In this study, decapitation was observed to result in the outgrowth of such lateral buds, reflecting a three-fold increase in the number of nodes arising from branches - which otherwise produced only one leaf per branch. The total number of nodes per plant was unchanged by removal of the growing tip, however, reflecting a decrease in the number of nodes on the main stem due to decapitation. Bauer et al. (1976) have presented similar findings for field-grown soybeans. In addition, these authors reported that the dry weight of the vegetative organs was decreased by removal of the terminal bud, while seed yields remained fairly constant. Similarly, the dry weight of vegetative organs was found to be decreased by decapitation in this study; but overall seed yields, on the other hand, were increased.

Such increases in total seed yield are consistent with the findings of other authors for several grain legume species (Stewart, 1976; Clifford, 1979; Binnie and Clifford, 1980; Tayo, 1980; Tayo, 1982), though the origin of these increases were in some cases different from those reported here. For both pigeon pea and soybean, Tayo (1980, 1982) reports significant increases in yield due to the production of more and/or heavier pods. Stewart (1976) reported an increase in all yield components over the control plants for a treatment performed at the same stage of growth as the one reported here, but for cowpea cv. K2809. For that cultivar, increases in the number of pods were reported. Only a

slight increase was observed in the present study; but this, combined with a greater number of seeds per pod, resulted in a 34% increase in total seed yield. In light of a significantly lower weight of vegetative components - which is well reflected in a 42% increase in the harvest index of decapitated plants over controls, increased yields were clearly not a reflection of increased vegetative growth.

Such was not the case for plants which, upon decapitation, were treated with benzyladenine applications to the axillary buds. In this case, seed yields were increased concommitant with increased vegetative yields. In comparison with plants which were only decapitated, the number of nodes appearing after treatment was enhanced by application of benzyladenine to the axillary buds. As with plants which were only decapitated, nodes origininated from the side branches at approximately 3 per branch, but for more branches. This resulted in a significantly greater final node number than that of plants which were only decapitated, and 18% more nodes were produced by plants treated in this fashion than by control plants.

Decapitation is known to enhance the metabolic and physiological processes of remaining shoot material, which is manifested by increased metabolic activity (Phillips et al., 1969; Meidner, 1970; Carmi and Koller, 1979) and increased growth (Carmi and Koller, op cit.; Binnie and Clifford, 1980) in remaining organs. The repeatedly observed phenomenon of lateral bud outgrowth in many studies, including the present one, is in itself an attestation to this effect.

Cytokinin application to leaves is also associated with the enhancement of metabolic activities at the site of application (Scott

and Liverman, 1956; Adedipe et al., 1971; Carmi and Koller, 1978). The similarity in response of cytokinin appplication to dormant axillary buds and decapitation (Wickson and Thimann, 1958; Sachs and Thimann, 1967; Schaeffer and Sharpe, 1969; Ali and Fletcher, 1971) has led to the suggestion that decapitation increases the availability of cytokinins to the remaining shoot material by reducing competition between shoot organs for cytokinins from the roots (Wareing et al., 1968; Katagiri and Tsuji, 1980). Accepting that such a mechanism may have underlain the enhanced branch outgrowth of the decapitated plants in this study, additional cytokinin application to the axillary buds at the time of decapitation was found to further increase the growth of these branches. This is consistent with the apparent metabolite-mobilizing effects of this group of synthetic hormones (Mothes and Englebrecht, 1961; Leopold and Kawase, 1964) and their ability to enhance metabolic activities at the site of application.

Metabolite mobilization and the enhancement of metabolic activities at the site of application may indeed have been responsible for the effects observed for foliar applications of benzyladenine, whether the plants were left intact, or decapitated prior to benzyladenine sprayings. In both of these cases, relatively little vegetative weight was accumulated (about 50% of that of the control) and it can be assumed that the majority of this decrease was a reflection of post-treatment reductions in vegetative accretion. When decapitation was combined with the foliar benzyladenine spray, branching effects were similar to those of decapitation alone. A reduction in total vegetative weight due to the sprays, however, may have been a reflection of reduced growth of

the new leaves and stems associated with these branches, while the sprayed leaves of the main axis (which had already expanded at the time of treatment) may have mobilized plant resources and limited new growth. This explanation is consistent with the observations of Leopold and Kawase (1964) in which a leaf treated with benzyladenine brought about the inhibition of growth in other untreated leaves on the same plant. In the present study, this effect was even more pronounced. When intact plants were sprayed with benzyladenine, comparatively few new leaves were initiated, while internode elongation was reduced three-fold and vegetative accretion was decreased by nearly 50%.

In comparison to the control plants, total grain yields were not affected by either of the benzyladenine foliar spray treatments, despite a lower amount of vegetative growth. These treatments did not however match the yields of the plants which were only decapitated and yielded 40% more grain weight. Reductions due to foliar spray applications of benzyladenine were clearly a reflection of fewer seeds per pod rather than any other yield component, and this may have been a function of a reduced ('source-limiting') photosynthetic area. Perhaps the afore-mentioned mobilization effects on the leaf area were still operant at this period of growth. No accounts were found by the author regarding such duration of effect, however. Further, assumed enhancement of photosynthetic activity (Adedipe et al., 1971) might have proven favorable to pod and seed development.

With similar grain yields and much lower vegetative yields, the harvest indices of the plants sprayed with benzyladenine were more than 30% greater than those of the control plants. This is not in agreement

with the observations of other authors (Okelana and Adedipe, 1982) who have observed lower harvest indices after benzyladenine applications to young cowpea plants. In that study much lower concentrations of benzyladenine (about 40 - 4000 times lower than those of the present study) were used, however. In a number of floricultural crop studies, the only type of studies resembling this one in terms of concentration range, the bushy, compact growth of the plants described and pictured (Carpenter et al., 1971, 1972; Jackson, 1975; Jeffcoat,1977) were far more consistent with the findings of this study,

Unlike the responses observed for the decapitation/ benzyladenine treatments, applications of TIBA at early flowering had little effect on the vegetative yield of the plants. In the controlled environment studies, no significant differences in vegetative/ branching components were observed. It may be fair to assume that effects on apical dominance per se were minimal in comparison to those obtained in the other studies reported here. Indeed, very few of the variables under study for TIBA-treated plants in the controlled environment experiment reported here were found to differ from those of the control plants. However, the pilot study revealed that optimal concentrations of TIBA significantly increased the majority of yield components in the greenhouse environment. The increases in total seed yield (44%) observed here were superior to those observed previously for cowpea (Hipp and Cowley, 1969), which were closer to those observed for the controlled environment study. Rather, the yield increases observed for the pilot sudy were closer in magnitude to those observed in a number of studies performed with other grain legume species (Sinha and

Ghildiyal, 1973; Tanner and Ahmed, 1974; Chowdhury et al., 1978; Reddy and Zaheda, 1979). As in this study, much of this yield increase was attributed to increases in pod and seed numbers.

The differences in yield response observed between the pilot study and the controlled environment study in the TIBA experiments are not atypical of research conducted with TIBA, the responses to which are multifarious and often strongly influenced by climatic variables and plant variety (Greer and Anderson, 1965; Burton and Curley, 1966; Hicks et al., 1967; Bauer et al., 1969; Hume et al.,1972).

3.8 Conclusion

Crop plants have been subjected to differing selection pressures during their evolutionary history following domestication and certain changes have characterized the evolution of most seed crops. Among these changes are the loss of seed dispersal mechanisms, increases in seed and leaf sizes, development of determinate or compact growth habits, shifts in life cycle to annuality and shorter duration, changes from outbreeding to inbreeding, and a general loss of sensitivity to the environmental signals that previously regulated development (Lush and Evans, 1981).

Domestication involves conscious selection, and, in most centres of crop domestication and major migration, the cereal grains have not only received the most attention, but have also been grown on relatively more fertile land, and, in general, been afforded the major part of limited agronomic inputs. Grain legume crops, by contrast, have been traditionally grown on marginal lands of poor fertility. Hence, despite probable millenia of cultivation, the majority of pulse species are still grown in conditions which differ little from their native habitats. With natural selection having continued to exert a major effect on these crops' evolutions, selection pressures on pulses have been for adaptation to stress conditions such as drought, poor fertility, and competition with biotic agents (pests, pathogens, and weeds) (Jain and Mehra, 1980).

Such an evolutionary history of stress after domestication has favored the survival of cultivars with characteristics such as bushy,

spreading, and indeterminate growth habits, photo and thermosensitivity, and a protracted crop duration. Further, these species are characterized by a profligate loss of reproductive structures in response to environmental/ biotic stresses and even in more optimal conditions (Ojehomon, 1970; Stewart, 1976; Summerfield and Wien, 1980).

Though these adaptations are undeniably favorable to provision of yield insurance under prolonged or even ephemeral duress, such attributes bear little resemblance to the the ideotypes we now associate with large-yielding cereal varieties grown with improved agronomic management (Jain and Mehra, 1980). Selected for large biological versus economic yields, the pulses fail to exploit their capacity for large dry matter production by correspondingly large seed yields. Consequently, the majority of these species have small harvest indices and respond poorly to increased population density.

If a crop plant is capable of heavy dry matter production, it is agronomically important that it render a maximum part of that yield as the useful product. The harvest index relates the effectiveness of the formation of the economic part of yield to total yield. Each of the treatments in the decapitation/ benzyladenine experiment increased the harvest index over that of the control. In the one case in which this increase was not significant - that is, decapitation plus application of benzyladenine to the axillary buds, a significant increase in yield was associated with a greater production of vegetative matter. Hence, either actual increases in yield or increases in harvest indices over control plants were observed for the treatments in this study.

There apppears to exist an optimum level of leaf area accretion

for the best performance in terms of seed production by grain legumes (Adams, 1974). The performance of treated plants here appears to suggest that the 'normal' condition of this cowpea cultivar is hardly optimal in terms of seed production. The treated plants are, of course, manipulated artefacts, but do indicate that better seed yield might be expected from equal or lesser quantities of vegetative accretion. For decapitation alone, and both treatments involving a foliar benzyladenine spray, vegetative growth was restricted but not to an extent that photoassimilate supply to the seeds was impaired. The treatments in fact led to a more efficient dry matter partitioning between reproductive and vegetative components, possibly by reducing competition for photoassimilates and nitrogen.

The plants resulting from the treatments imposed here represent modifications of the Vita-5 genotype. It can be suggested that improvements resulting from these treatments were at least partly due to alterations of apical dominance. The concept of apical dominance control in young plants for increasing productivity is not a new one. Indeed, the practice of pinching young plants is even recommended for a number of vegetable species in gardening manuals (Biggs, 1980) and is a common practice with several floricultural crops (Jeffcoat, 1977).

The immediate significance of the findings reported here may lie in the context of plant growth regulation. The 'one-shot' foliar spray application of benzyladenine reported here, though it did not result in a yield increase per se, siginificantly checked excessive vegetative growth and resulted in greatly improved agronomic productivity. Further, though no data were presented, the picture presented in Plate

3 clearly demonstrates a more easily harvestable product, with pods sitting well above the leaf canopy. The significance of this might be even more evident in high-density field plantings.

It is well recognized that the primary goal of plant growth regulators is the increased bioconversion of solar energy to harvested components (Hardy, 1978). Furthermore, though plant growth regulator use has hitherto been confined to small, high-value horticultural crops - as management aids, agrichemicals, due to the high cost of their development and registration, can now only be seen to have a commercially viable future in the larger markets provided by the 'broad-acre' agronomic crops (Batch, 1981).

Indeed a number of cytokinin-containing commercial preparations already exist. In the context of apical dominance control, use of chemical pinchers - selective inhibitors of shoot tip development - might yield results similar to the decapitation performed in this study.

Reports on the future of plant growth regulation in grain legume production paint a bleak picture for this crop management component (Summerfield et al., 1978). It is true that though the effects of numerous chemicals with potential 'growth regulating activity' have been evaluated over the past thirty years, there are no compounds commonly used in current commercial soybean production (Egli, 1976). Furthermore, it is doubtful that plant growth regulators will ever have a place in peasant agriculture, and that though a short-term role may be found for plant growth regulators in more sophisticated agricultural systems, a permanent role might represent a failure in plant breeding (Summerfield et al., 1978).

In the latter context, the findings of this study may have significance as a probe of development processes worthy of genetic selection. If the findings of the cultivar screening are accurate, modifications of apical dominance might prove valuable for a number of cultivars, as the majority of those under study were subject to an inequitable yield distribution over the whole plant. Crop improvement might be achieved by incorporation of earlier branching and improved yield efficiency of the lower crop canopy.

The findings of this study might indeed be extended over a number of genotypes (including some of more determinate growth habit) and over a variety of environments to further evaluate or elucidate a possible yield-limiting role of apical dominance.

4. EXPERIMENT SERIES 2. A MODEL FOR INTERNODAL COMPETITION BETWEEN REPRODUCTIVE COMPONENTS OF COWPEA CV. VITA 5

4.1 Introduction

In Section 2, it was observed that for cowpea cultivar Vita-5, as many as 60% of the primary yield component sites (peduncles), which became productive failed to contribute to yield. Peduncle activity for these sites was either arrested (that is, there was a cessation of peduncle activity), suppressed (that is, peduncles came into activity only when more active sites had reached pod maturity), or ceased (that is, the peduncles abscised). Consequently, relatively few peduncles became and remained reproductive.

Based on anatomical studies, Adams (1967) has suggested that the dwarf french bean plant is composed of several independent nodal units each comprising two trifoliate leaves. The view of a single plant as a population composed of modules such as leaves and associated axillary buds has been put forward in a number of studies, and Doust and Eaton (1982) presen findings for the existence of such demographic attributes for the reproductive components of beans.

While several studies support the existence of 'competitive inhibition' from older fruits with respect to later-formed ones (Van Stevenick, 1957; Tamas et al., 1979b), very little evidence exists to suggest that such competitive inhibition may be involved in other expressions of failure to become and remain reproductive, such as that

observed here.

In this series of experiments, a model for internodal competition between reproductive components in modified cowpea plant systems will be presented by studying the distribution of ^{14}C between reproductive components of allegedly differing abilities to 'attract' assimilates.

4.2 Materials and Methods

4.2.1 Preparation of the air mixture and exposure apparatus A Canadian Liquid Air size 3 compressed gas cylinder was used as a reservoir for the $^{14}CO_2$ air mixture. To load this cylinder with air having about 350 ppm CO_2, 3.68 mmol CO_2 were generated from the reaction of 0.4 mmol $Ba_2{}^{14}CO_3$ (2.0 mCi of $Ba_2{}^{14}CO_3$ with a specific activity of 5.0 mCi/mmol CO_2) and 3.28 mmol K_2CO_3 (453 mg) with an excess (20 mls) of 90% formic acid in the bottom of a closed vacuum flask. The flask was connected in series to the evacuated master cylinder with a flow meter adjusted to deliver 300 cc/min. The master cylinder was allowed to draw air from the flask until it had reached atmospheric pressure, at which time the valve was closed. The air within the cylinder, high in $^{14}CO_2/CO_2$ concentration, was then diluted with a CO_2-free synthetic mixture from a Canadian Liquid Air cylinder, adjusted to deliver 500 psi. The master cylinder hence contained an air mixture with CO_2 similar in concentration to that of normal air.

From this synthetic air mixture, lecture bottles were filled to 500 psi and used as the source of the $^{14}CO_2$-labelled air mixture to which plant leaves were exposed. The apparatus used to expose the leaves was based on that of Shimshi (1969) and obtained from the Biology Department of McGill University (Plate 4).

Plate 4

Apparatus for exposure of leaves to $^{14}CO_2$

(a) photosynthesizing chamber

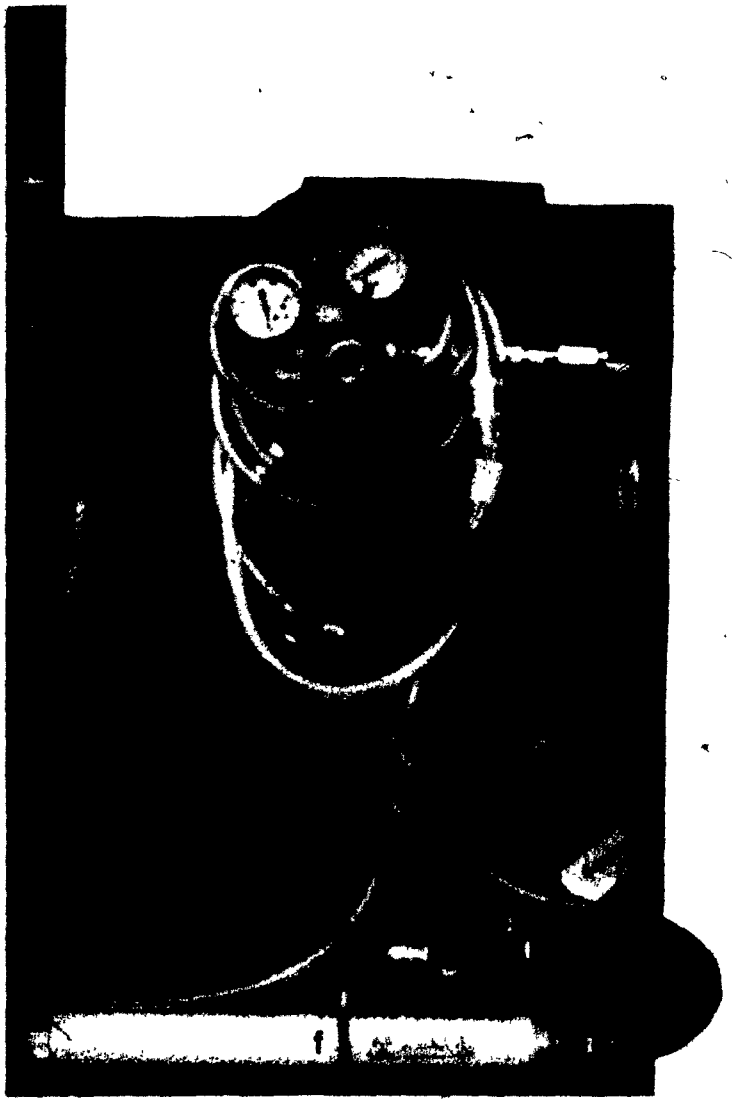
(b) air reservoir

(c) pressure gauge

(d) three-way valve

(e) CO_2 trap

(f) clean air evacuation system



4.2.2 Plant material All experiments were conducted on reproductively active 40-50 day old plants (uniform age within each experiment) which were grown under the controlled environment conditions described previously (Section 3.2), but in twelve cm pots, which yielded plants approximately 25 cm high and more manageable for this type of experimentation.

From each plant, and depending on the experiment, one (or two) reproductively active peduncle(s) was/were selected. The plants were then stripped of all leaves and peduncles, except for the chosen peduncle and its (their) subtending leaf(ves), in a fashion similar to that used by Williams and Marinos (1977) for Pisum sativum. All peduncles (except when flowers and/or pods were retained) were decapitated. When flowers were retained, these were chosen such that they would open during the first twenty-four hours after exposure to $^{14}CO_2$. Plants with three day-old pods were chosen for all treatments in which pods were used.

4.2.3 Hormone preparation and application to the peduncle stumps The IAA employed to direct the movement of ^{14}C labelled products was first dissolved in the lowest possible quantity of an appropriate solvent (95% ethanol) and then diluted with heated lanolin to the desired concentrations. These solutions were poured hot into 5 cm petri dishes to a depth of 1.5 cm, stirred, and refrigerated. Large black straws (0.7 cm diameter milkshake straws which were spray-painted black three times) were cut to the required peduncle length and pressed into the

hardened hormone/solvent/lanolin suspensions (or solvent/lanolin suspensions when lanolin was used alone). The resultant congeled suspensions - 0.7 cm in diameter and 1.5 cm deep, in the straws, were applied to the decapitated peduncle stump ends with the whole of the peduncle length hence covered by a black plastic barrier, preventing light interception by the peduncle (Appendix C2).

4.2.4 Exposure to $^{14}CO2$ and measurement and expression of ^{14}C distribution Twenty-four hours after hormone application to the peduncle stumps, the leaf subtending the peduncle on each plant was set up in the photosynthesizing chamber (with the lower epidermis facing the circulating air and the upper epidermis facing the light) for ten minutes under a fluorescent light source (approximately 100 microeinsteins/m^2/sec). Following this exposure, the plants were left in the fume hood under fluorescent lights (approximatley 90 microeinsteins/m^2/sec) for photosynthate distribution for 24 hours. This period was determined prior to experimentation (Appendix C1). After this period, the plants were cut at the soil line and divided into component parts - stem, leaf, and peduncle. These were oven-dried for 30 hours at 70^{0}C in a forced-air drier, after which they were weighed (Wein et al., 1976; Kuo et al., 1978). Assayed samples consisted of three finely-ground (0.5 mm mesh) 20 mg samples of tissue for each plant part, when enough tissue was available.

The samples were prepared for liquid scintillation counting using a method described by Mahin and Lofberg (1966) with modifications. For

each sample, tissue digestion and bleaching were performed by adding 0.5 mls of a 2:1 solution of 30% hydrogen peroxide and 60% perchloric atid to the dried tissues in 20 ml scintillation vials, and heating the sample vials for two hours at 70°C. The sample vials were then cooled to room temperature and the digested samples were brought to counting state by dilution with 15 mls of scintillation fluid and agitation. The scintillation fluid was formulated by dissolving 0.3 g of 2,5-diphenyloxazole (PPO) in a 750 ml solution of toluene and 2-ethoxyethanol (500 ml : 250 ml).

Measurements were performed in a Tri-carb liquid scintillation spectrometer, model 3000 series, Packard Instrument Co., equipped with automatic external standardization. The counts obtained were quench-corrected and converted to disintegrations per minute (dpm).

Despite the similarity of size, age, and fruiting characteristics of the plants and the organs that were used, ^{14}C uptake varied greatly from one plant to another (Appendices C5 and C6), and actual counts could not be used for data analysis. Hence, the activity of the plant parts (dpm/ 20 mg sample) were averaged for the three samples and the percentage of total recovered activity for each plant part was obtained by multiplying this value by the plant part dry weight and dividing this by the total activity recovered from the plant.

4.3 Experiment 1. The mobilizing potential of pods, flowers, and IAA applied exogenously on peduncle stumps.

4.3.1 Materials and methods An experiment was conducted to determine the potential of various treatments to accumulate ^{14}C-assimilates. The materials and methodology used were those described in Section 4.2, using the leaf and reproductive organs situated at the third main stem node of the plants. A completely randomized design comprising 6 treatments and 3 replicates of each treatment was utilized:

(a) one three-day old pod was maintained on the peduncle;

(b) one flower was maintained on the peduncle;

(c) the peduncle was decapitated just below the floral cushion and lanolin (an ethanol/lanolin suspension) was placed on the decapitated peduncle stump;

(d) the peduncle was treated as in (c) except that 10 ppm IAA (an ethanol/IAA/lanolin suspension) was placed on the decapitated peduncle stump;

(e) the peduncle was treated as in (c) except that 100 ppm IAA (an ethanol/IAA/lanolin suspension) was placed on the decapitated peduncle stump;

(f) the peduncle was treated as in (c) except that 1000 ppm IAA (an ethanol/IAA/lanolin suspension) was placed on the decapitated peduncle stump.

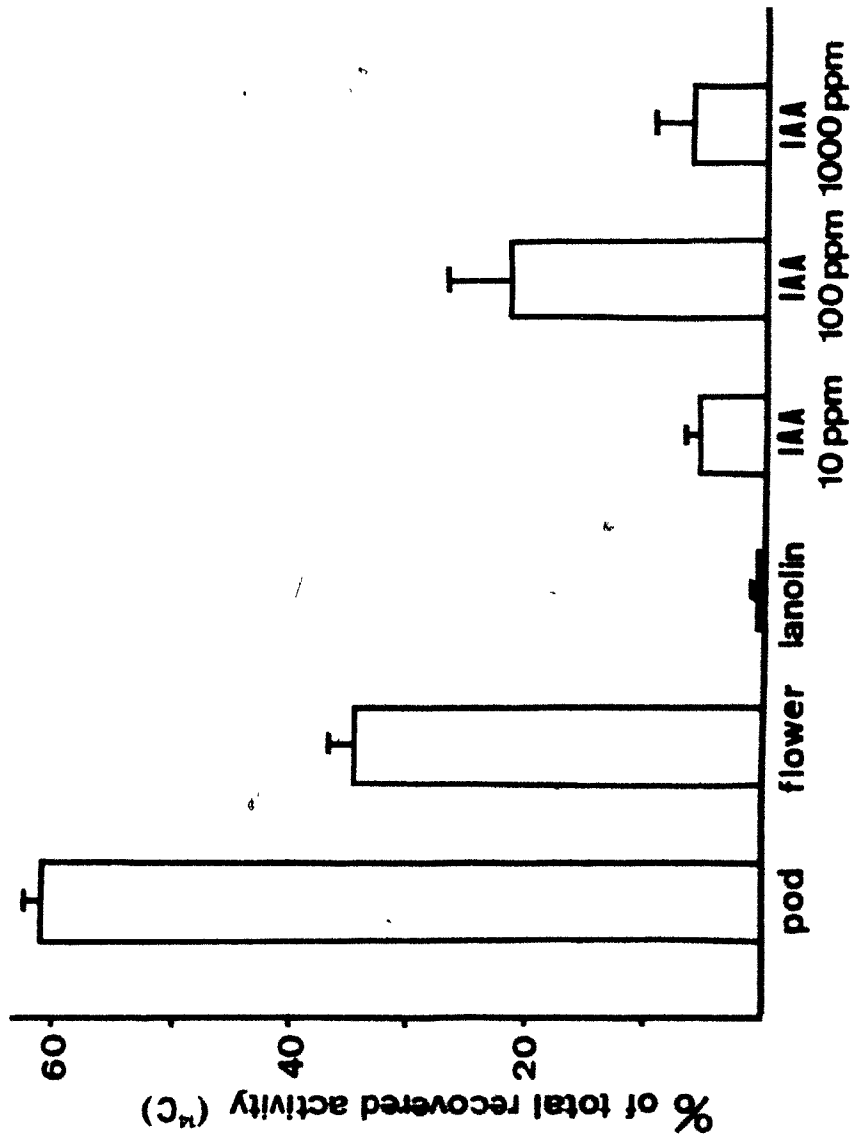
4.3.2 Results Results are presented in Figure 7 and Appendices C3 and C5. The presence of a three-day old pod resulted in the greatest accumulations observed here for a reproductive unit (peduncle + reproductive organ/ or hormone). The presence of a flower also resulted in the accumulation of large amounts of ^{14}C assimilates, though this was approximately 27 percentage points less than that of a three-day old pod. Lanolin applied to the peduncle stumps resulted in only negligible accumulations of ^{14}C assimilates, while the presence of any of the concentrations of IAA in the lanolin suspensions resulted in marked increases in the accumulation. The greatest increase occured when the concentration of IAA in the lanolin suspension resulted in marked increases in the accumulation. The ability of this treatment to cause accumulations of ^{14}C assimilates was, at approximately 22% of all assimilates, lower than that of a three-day old pod or a flower. This concentration, however, was chosen as the optimum concentration (of those under study) for use in the subsequent experiment.

The ability of the reproductive units treated with IAA to accumulate ^{14}C assimilates was subject to a good deal of variation (Appendices C3 and C5). This type of variation is not uncommon among experiments of this type (Davies et al.,1966; Seth and Wareing, 1967; Hatch and Powell, 1971). Hence, in these types of experiments, it would appear safer to refer to trends rather than absolutes. Suffice it to say that though no clear-cut trend in the ability of increasing concentrations of IAA to attract ^{14}C-assimilates was observed, the presence of IAA in the lanolin

Figure 7

^{14}C activity recorded by peduncle unit (expressed as % of total activity recovered by plant) of cowpea cv. Vita-5 subjected to a number of treatments (refer to Section 4.3.1) (means of three replicates)

$\top$ = Standard error


% of total recovered activity (^{14}C)
60
40
20
pod
flower
lanolin
IAA
10 ppm
IAA
100 ppm
IAA
1000 ppm

was characterized by a greater ability to accumulate ^{14}C assimilates than that of lanolin alone.

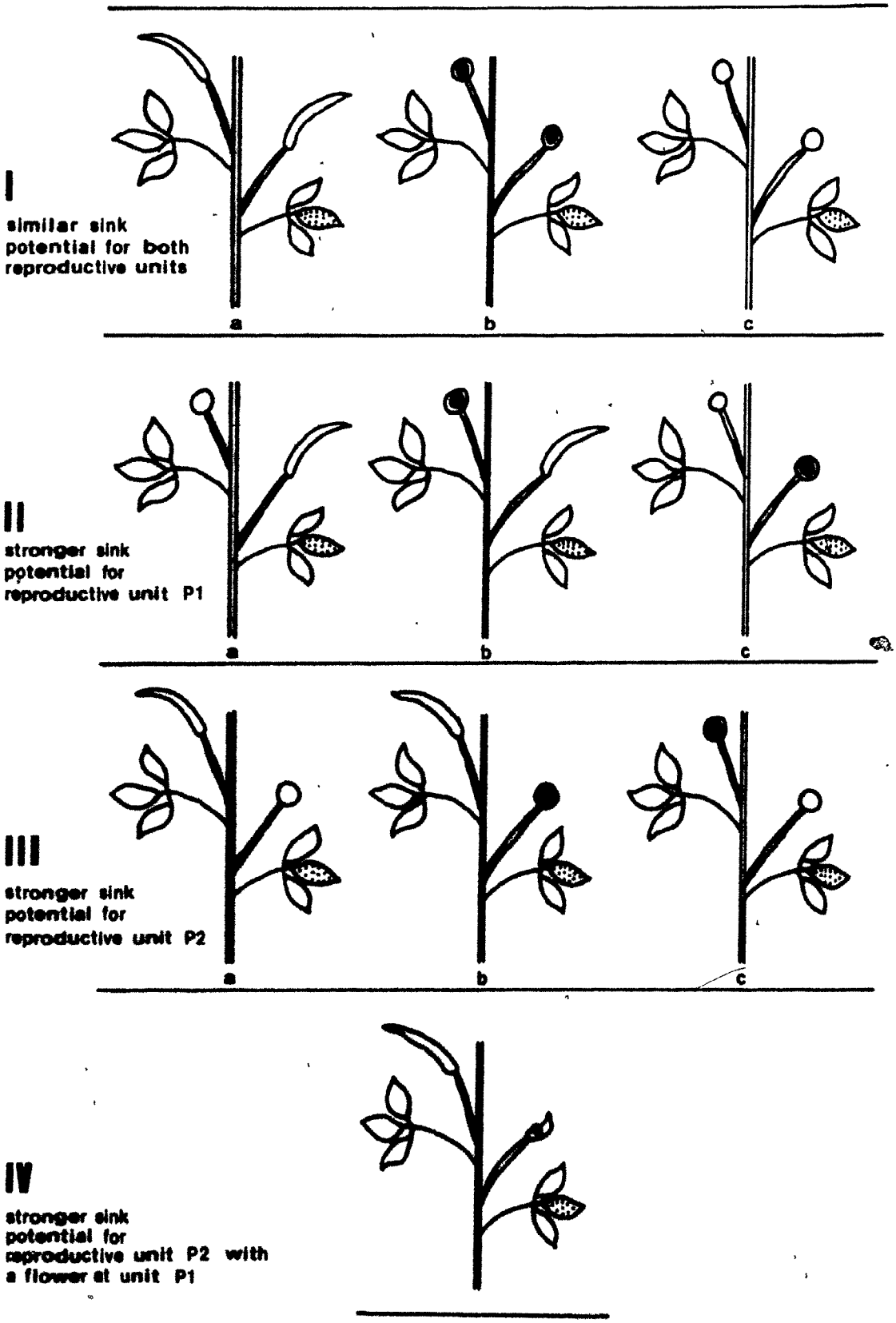
This experiment was performed in order to establish a baseline of response for use in the subsequent experiment. Hence, reference to these treatments in the future will be in terms of fairly established responses such as 'greater sink potential', 'greater mobilizing ability', or 'sink strength'; the presence of 100 ppm IAA in a decapitated peduncle stump, for example, creating a greater sink potential than the presence of only lanolin, but a lesser sink potential than that of a 3-day old pod.

4.4 Experiment 2. The effect of two reproductive units of varying mobilizing potential at two different nodes on the distribution of ^{14}C-assimilates from a given leaf

4.4.1 Objectives This experiment was conducted in order to determine the effects of varying mobilizing potentials (as established in Section 4.3) of two reproductive units on the distribution of ^{14}C-assimilates from a given leaf, in a plant system comprised of two nodal units

4.4.2 Materials and methods The materials and methodology used were those described in Section 4.2, using the leaf and associated reproductive unit situated at the third and fourth main stem nodes of the otherwise totally pruned plants. A completely randomized design comprising ten treatments (presented diagrammatically in Figure 8) and three replicates of each treatment was utilized.

4.4.3 Results Results are presented in Appendices C4 and C6 and Figures 9 and 10, with the first figure presented to give an overall picture of ^{14}C-distribution throughout the aerial portions of the plant twenty-four hours after exposure of the fed leaf and Figure 10 presenting a more precise picture of results obtained.


I
similar sink potential for both reproductive units
a
b
c
II
stronger sink potential for reproductive unit P1
a
b
c
III
stronger sink potential for reproductive unit P2
a
b
c
IV
stronger sink potential for reproductive unit P2 with a flower at unit P1

for the reproductive units. When three day old pods were present at both nodes, the reproductive unit at position 1 (P1) accumulated approximately 38% of the assimilated ^{14}C, while that of position 2 (P2) accumulated about 5% of the total ^{14}C (Figure 9.I.a). This accumulation of a greater proportion of ^{14}C by P1 was consistent across all the other treatments in which the 'sink potential' (as established in Experiment 1 of this series) was allegedly the same (or similar) for both positions (Figure 9.I.a-c). For treatments Ib and Ic, where the mobilizing abilities were less pronounced (b) or essentially non-existent (c), the proportion of ^{14}C retained by the fed leaf was much higher (77% and 66% respectively, versus 38% for treatment Ia). The fed leaf in fact retained a greater proportion of ^{14}C assimilates in all cases in which no actively growing pod was present at either node (Figure 9.I.b,c; II.c; III.c), though this was less noticeable when IAA was present in the lanolin applied to the peduncle stump.

The results of the second series of treatments (presented in Figure 9.II.a-c) reveal that when sinks of a stronger mobilizing potential were present at P1, and particularly when this was a pod, there was a good deal of movement of ^{14}C assimilates out of the fed leaf, but relatively little ^{14}C was mobilized by stem tissues, the other leaves, and the P2 reproductive units. Movement to the latter position was low in all of these cases, though it was stronger when IAA was present in the lanolin applied to the peduncle stumps.

When a pod was present at the P2 position (Figure 9.III.a,b;

Figure 9

% of total activity recovered by plant parts,

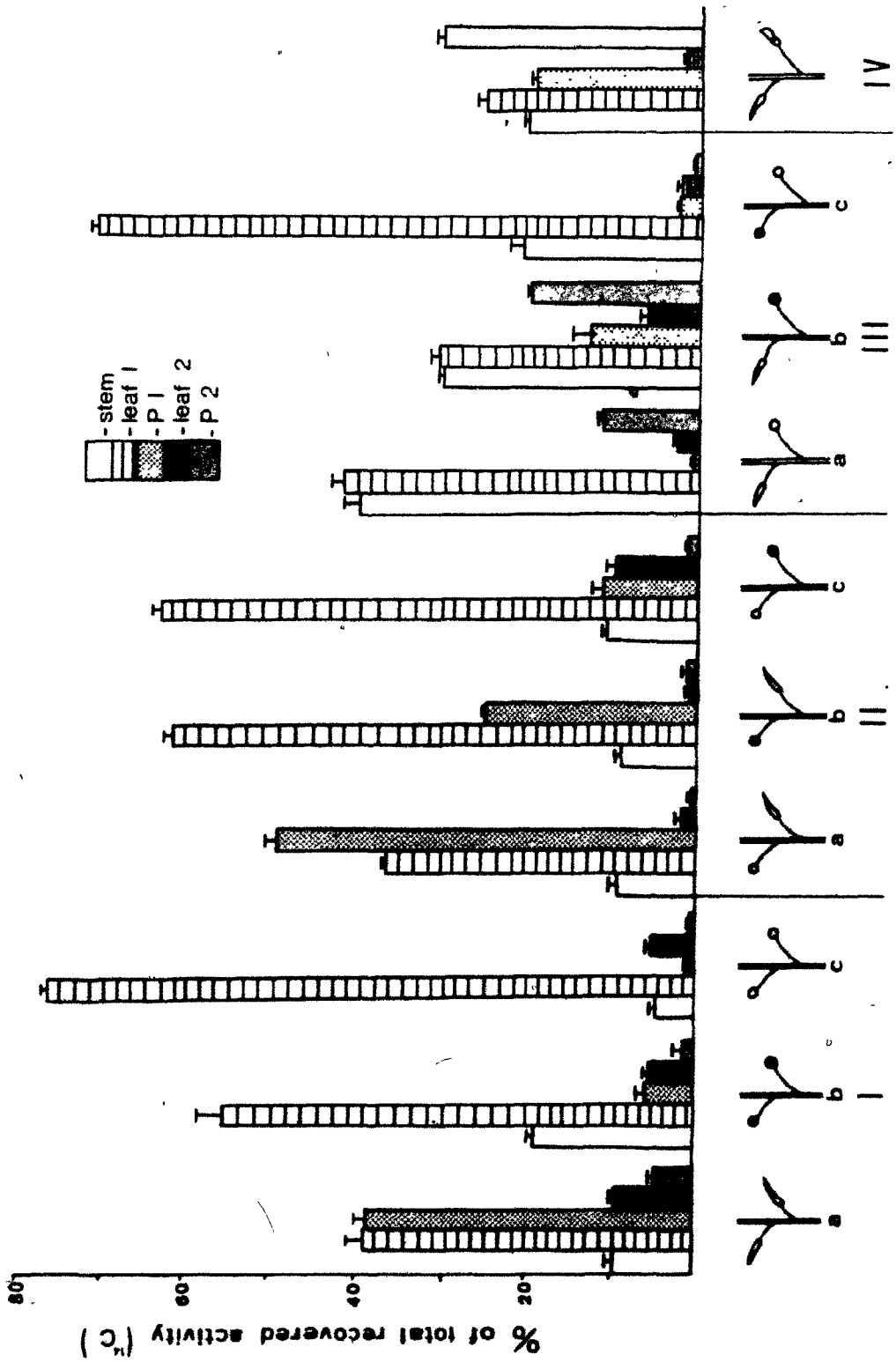
for plants of cowpea cv. Vita-5 subjected

to various treatments

(refer to Figure 8)

(means of 3 replicates)

$\top$ = standard error


% of total recovered activity (^{14}C)
80
60
40
20
- stem
- leaf 1
- P 1
- leaf 2
- P 2
I
II
III
IV
a
b
c

IV.), there was a good deal of ^{14}C movement out of the fed leaf, and, in addition to being mobilized by the reproductive units, a good deal of the ^{14}C assimilates were observed to be present in the stem tissues. This latter trend, though slightly less pronounced, was also observed when IAA in lanolin was applied to the P2 unit and when only lanolin was applied to the decapitated peduncle stump at P1 (Figure 9.III.c).

A greater accumulation of total recovered activity by the reproductive units was observed when actively growing pods were present at the reproductive sites, as better evidenced in the summarized findings presented in Figure 10. This was found to be particularly true when the pods were located at the P1 position, wherein the reproductive units accumulated 27-50% of the assimilated ^{14}C, of which no less than 88% was mobilized by the reproductive unit at position 1 (Figure 10.I.a; II.a,b;III.a,b).

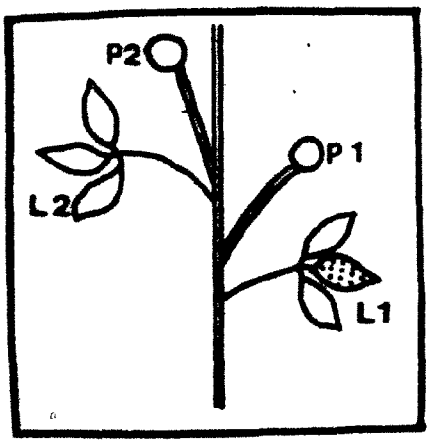
The results of the first series of treatments presented in Figure 10 clearly demonstrate the mobilizing abilities of the various treatments, with pods at both positions accumulating 43% of the ^{14}C-assimilates and with lanolin applications to the peduncle stumps accumulating only 2.6% versus a 9.6% accumulation occurring when IAA was present in the lanolin.

It is also obvious from the results of this same series (Figure 10.I) that when sinks of relatively the same mobilizing potential were present at both of the reproductive unit positions, the reproductive unit associated with the fed leaf obtained by far the greater proportion of the ^{14}C assimilates mobilized by these

Figure 8

Diagrammatic representation of treatments

Series 2, Experiment 2:



L1 = leaf at position 1 (node 3)

L2 = leaf at position 2 (node 4)

P1 = reproductive unit at position 1 (node 3)

P2 = reproductive unit at position 2 (node 4)

= fed leaflet

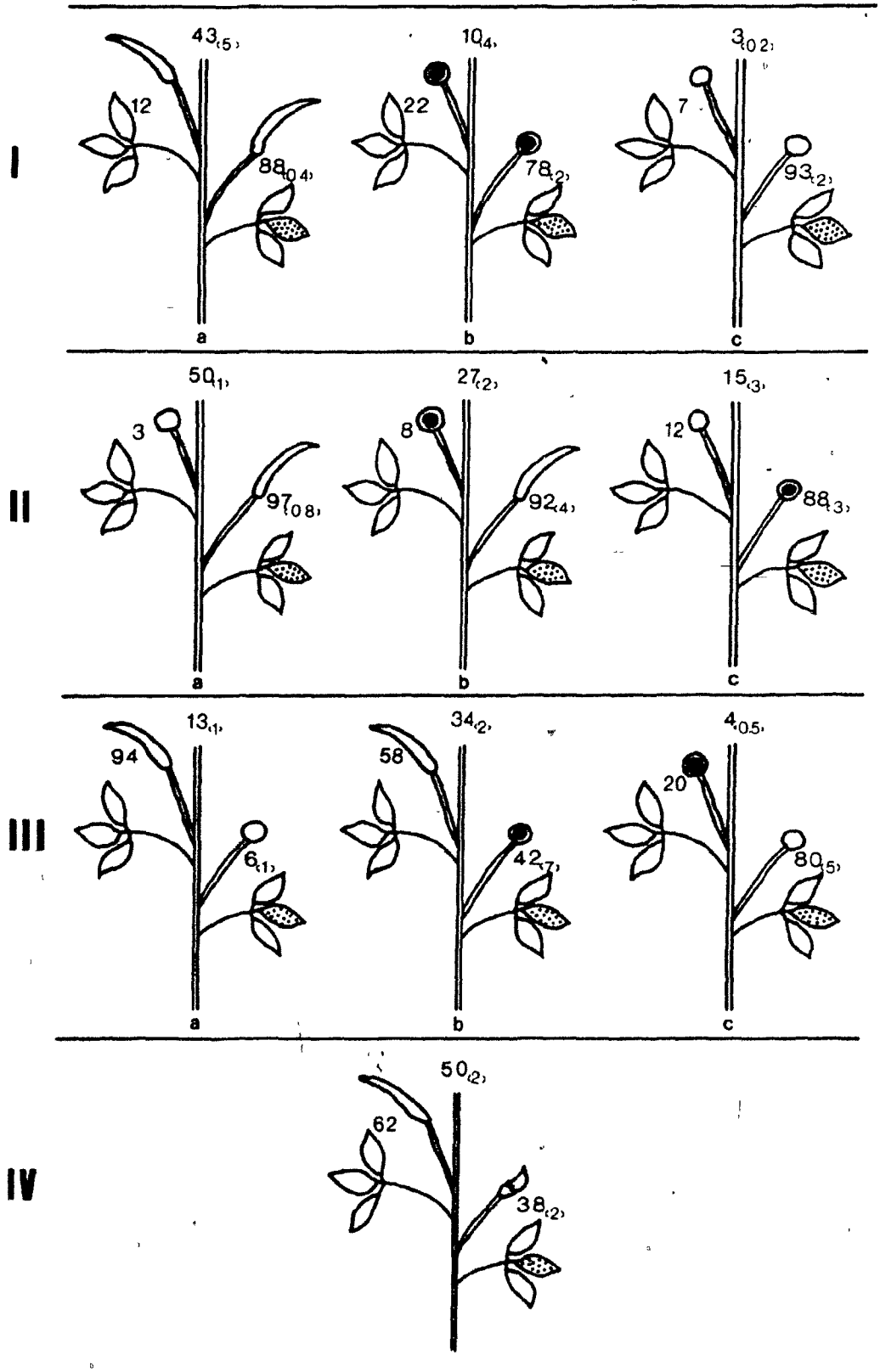
= peduncle

= three day old pod

= applied lanolin on decapitated peduncle stump

= applied IAA in lanolin on decapitated peduncle stump

= flower


I
43(5)
12
88(0.4)
a
10(4)
22
78(2)
b
3(0.2)
7
93(2)
c
II
50(1)
3
97(0.8)
a
27(2)
8
92(4)
b
15(3)
12
88(3)
c
III
13(1)
94
6(1)
a
34(2)
58
42(7)
b
4(0.5)
20
80(5)
c
IV
50(2)
62
38(2)

units - the P1 position accumulating no less than 71% of the total.

Not surprisingly, the same effect was observed to be even more pronounced when the P1 reproductive unit was of a stronger sink potential than that of the P2 (Figure 10.II.a-c). The situation differed when the reproductive unit at position 2 was of a stronger sink potential than that of P1, the effect being dependent on the mobilizing potential of the P2 reproductive unit (Figure 10.III.a-c; IV.). Hence, though an IAA in lanolin treatment applied to the peduncle stump resulted in the accumulation of only 20% of the ^{14}C assimilates by the reproductive units even when the mobilizing potential of the P1 position was low (lanolin alone), the presence of a three day old pod at the P2 position resulted in an accumulation of 94% of the ^{14}C assimilates found in these parts (Figure 10.III.c and a, respectively). When a treatment of greater mobilizing potential (IAA + lanolin) was applied to the P1 position, the P2 reproductive units accumulated 56% of the ^{14}C assimilates (Figure 10.III.b).

This latter finding is analagous to that observed when a three day old pod was present at the P2 position and a flower was present at P1 (Figure 10.IV.). In this instance, the presence of a three day old pod at the P2 position resulted in an accumulation of 62% of the ^{14}C assimilates, while the flower and peduncle accumulated 38%; the combined total of activity recovered by these two reproductive units being approximately 16% higher than when the hormone in lanolin treatment was used at the P1 position.

4.5 Discussion

The partition of assimilates within a plant appears to be determined by the various 'sinks' which arise either from assimilate utilization for growth or accumulation in the form of insoluble reserves (Wareing,1978). Important sinks for the photosynthates acquired by CO_2 fixation by mature leaves are such areas of active growth, notably: expanding leaves (Webb and Gorham, 1964; Williams, 1964); growing meristems (Aronoff, 1955); storage organs (Burt, 1964; Geiger, 1966); and growing fruits (Brown, 1968; Ashley, 1972; Harvey, 1973; Kipps and Boulter, 1973; Wien et al., 1976; Williams and Marinos, 1977).

Despite the absence of any generally accepted criteria for measuring 'sink strength', the ability to accumulate photosynthetically produced carbon assimilates can be interpreted to be a fairly good reflection of a sink's strength potential. Though, as indicated above, it is generally recognized that developing fruits and storage organs are important sinks for plant resources, the flower has received less attention and is not thought to be a powerful sink (Hale and Weaver, 1962). Nonetheless, experiments with carnation have shown that as much as 70% of the ^{14}C exported from a leaf treated with ^{14}CO may move into the flower in less than a day (Harris and Jeffcoat, 1972). Similarly, in Experiment 1 of this series, the flower was found to accumulate photosynthetically produced assimilates, though to a lesser degree in terms of total accumulation than a three-day old pod.

Relatively little is known as to the determinants of the competitive ability of a sink, but each sink appears to be characterized

by a certain 'mobilizing ability' whereby it can 'pull' or 'attract' assimilates against the competing abilities of other sinks (Wareing, 1978). Hence, in this study, the three-day old pod may be seen as having had a greater mobilizing ability than that of the flower (Figure 7). Similarly, an artificial sink, such as that created by 100 ppm IAA in lanolin applied to peduncle stumps were capable of accumulating 38 times more ^{14}C-assimilates after twenty-four hours than those accumulated when only lanolin was present (Figure 7). The mobilizing abilities of the hormone-treated peduncle stumps (or the hormone itself) was at most 1.6 and 2.9 times less than that of the pods and flowers, respectively. These differential mobilizing activities were further observed when two reproductive units were present on each plant (Figures 9 and 10). A great deal of evidence exists to support the view that, for a number of crop species, the primary source of photosynthate for a fruit is the leaf subtending it (Ashley, 1972; Ezedinma, 1973b). This association has been observed, in particular, for a number of legume crop species: cowpea (Ojehomon, 1972); French bean (Lucas et al., 1976; Wien et al., 1976; Olufajo et al., 1982); field pea (Flinn and Pate, 1970); and garden pea (Linck and Sudia, 1960, 1962; Lovell and Lovell, 1970) using ^{14}C-labelled assimilates. While the leaves at a blossom node do appear to be deeply committed to nourishing subtended fruits, this association does not appear to be exclusive, for broad beans at least (Crompton et al., 1981). Furthermore, in dwarf French beans, pod assimilates have been shown to be obtained in some circumstances from distant sources, while carbon fixed at a given point has been found to be widely distributed throughout the plant (Olufajo et al., 1982).

For cowpea, Ojehomon (1972) reported that a leaf exported its ^{14}C-assimilates primarily to the inflorescence in its axil. In the present study, the reproductive unit associated with the fed leaf at node 3 was found to be the primary recipient of the translocated ^{14}C assimilate, when a stimulus of assumedly equivalent mobilizing ability was present at the reproductive unit at node 4 (Figures 9.I.a-c and 10.I.a-c). This effect was even more pronounced when the reproductive unit associated with the fed leaf at node 3 was of greater 'sink potential' (or mobilizing ability) than that of the reproductive unit at node 4 (Figures 9.II.a-c and 10.II.a-c). When the opposite was true and the reproductive unit located at node 4 was of greater 'sink potential' than that of node 3 (Figures 9.III.a-c; 9.IV; 10.III.a-c; 10.IV), the former was capable of mobilizing substantial proportions of the ^{14}C assimilates, though this depended on the relative mobilizing abilities of the sinks in question. In general, however a three-day old pod at the fourth node was capable of accumulating at least 56% of all ^{14}C assimilated by the reproductive units whether the alleged mobilizing stimulus provided by the other reproductive unit was fairly strong (Figure 10.IV.), weaker (Figure 9.III.b), or essentially non-existent (Figure 9.III.a). In addition, substantial quantities of the assimilates were translocated to the stems in these instances, which might represent greater quantities of ^{14}C assimilates in the process of being translocated to the pod at node 4 or the temporary storage of these for later use - the latter being a pattern observed in other species (Khan and Sagar, 1966; Ismail and Sagar, 1981).

The uptake of greater proportions of ^{14}C assimilates by a

reproductive unit distant from the fed leaf could be of some importance in light of the role which this leaf is thought to play. As stated before, this leaf is thought to be the primary exporter of photoassimilates to the inflorescence in its axil for cowpea. In a similar vein, Ezedinma (1973b) has observed that removal of some cowpea leaves at full bloom resulted in cessation of development and death of pods arising from the axils of these leaves. This would suggest that the normal development of such pods is dependent on the deployment of current assimilates from the leaves subtending them. Several experiments do in fact indicate that it is current photosynthesis during the reproductive period that is the major source of dry matter for seed yield in several legume species, rather than dry matter accumulated in other plant parts during the vegetative period and translocated from storage (Yoshida, 1972; Hume and Criswell, 1973; Egli and Leggett, 1976; Lucas et al., 1976; Wien et al., 1976); Kuo et al., 1978).

If then, an actively growing fruit at a distant node can sequester assimilates that might have been associated with the reproductive unit located at a given node, then this might 'starve' the developing reproductive structures at that node. Wien et al. (1976) refer to this type of internodal competition when plant parts compete for a limited supply of assimilates, and point to other work which lends support to the existence of competition for assimilates (Lovell, 1969).

Indeed, differential competing abilities have been demonstrated for a number of legume species, in that earlier-formed fruits appear to promote the abortion of younger reproductive structures, particularly when these are in the same inflorescence (van Stevenick, 1957, 1958,

1959; Tamas et al., 1979a; Huff and Dybing, 1980). Competition by fruits could conceivably affect all stages of reproductive development, and it has been suggested that competitive inhibition might be implicated in such widespread plant phenomena as the failure of flower formation, floral abscission, and early fruit drop (van Stevenick, 1957; Chan and Cain, 1967; Adedipe et al., 1976; Tamas et al., 1979b).

This type of competitive inhibition by developing fruts has also been associated with vegetative characteristics. Tamas et al. (1979a,) have demonstrated the apparent association of fruit growth to axillary bud dormancy in beans, and have postulated that developing fruits limited shoot growth by inhibiting axillary bud development, in addition to other inhibitory effects observed on later-formed fruits. Fruit development has also been reported to enhance senescence in leaves (Leopold et al., 1959) and apical meristems (Malik and Berrie, 1975). It is not inconceivable, then, that such competitive inhibition might have been responsible for the arrest, suppression, or abscission of peduncles observed for this cowpea cultivar (Section 2.3; Figure 3).

If this is in fact the case and a limited supply of assimilates exists, then the ability to sequester these assimilates might be determined by each sink's mobilizing ability. There is considerable evidence that endogenous growth substances may play an important role in this respect (Wareing, 1978).

The production of significant amounts of endogenous growth substances is well associated with actively growing flowers, fruits, and seeds (Haagen-Smit et al., 1946; Nitsch, 1955; Burrow and Carr, 1970; Jeffcoat and Harris, 1972; Pate and Flinn, 1977; Davey and Van

page 89 omitted in page numbering

Staden, 1978). Application of exogenous growth substances to non-growing tissues, by the same token, can lead to an increased movement of assimilates to the point of application. Specific examples of this include the migration of amino acids toward a 'kinetin locus' (Mothes and Englebrecht, 1961) and the movement of C-sucrose from a site several cm away to the point of hormone application on a decapitated mature (non-growing) internode of dwarf pea or bean (Booth et al., 1962; Davies and Wareing, 1965; Patrick and Wareing, 1973).

The idea that IAA-directed transport (the most studied hormone in this regard) is due solely to enhanced tissue growth at the site of application has been repeatedly disputed (Booth et al., 1962; Patrick and Wareing, 1972, 1973, 1976) and considerable evidence exists to suggest a direct involvement of IAA in the normal processes of phloem loading and unloading (Wareing, 1978).

It seems fairly clear that it is a phenomena in the sinks which determines the tendency of assimilates to collect there. Williams and Williams (1978) demonstrated that the enhanced accumulation of ^{14}C assimilate in peapods caused by pod warming was due both to an effect on ovule growth directly and to a 'remote effect' on the transport system - the nature of this effect possibly being hormonal.

The high levels of growth substances in developing flowers, fruits, and other actively growing areas in the plant lend support to this hypothesis (Jeffcoat and Harris, 1972; Pate and Flinn, 1977). The effect of exogenous applications of growth substances lead to further suggestions that the translocation of assimilates to developing fruits might be regulated, or at least moderated, by the presence of these

endogenously. Seth and Wareing (1967) observed that the application of IAA to a bean peduncle from which the fruit had previously been removed had the significant effect of enhancing the accumulation of ^{32}P by this peduncle after the isotope had been injected through the stem base. Similar observations were made in the present study (Figure 7) in which application of IAA enhanced the translocation of ^{14}C assimilates from the fed leaf over that of a lanolin control. As in the case of other studies this leads to the suggestion that auxin might have a key role in fostering assimilate flow to the growing peduncle or fruit. Consequently, different endogenous auxin concentrations might be responsible for the preferential movement of ^{14}C assimilates to certain areas, such as was observed here. Furthermore, if auxins (or any other growth substances) were to be involved in the mobilizing ability of a growing organ, this preferential movement might be responsible for the postulated competitive inhibition of peduncle activity.

The findings observed here were based on modified plant systems with many organs removed and can, at best, serve as a model of what might occur in an intact plant.

5. SUMMARY AND FINAL CONCLUSIONS

In light of the observation that the premature abscission of peduncles causes a great loss of theoretical yield potential in cowpea (Stewart et al., 1980), a series of studies was undertaken to gain a better understanding of this phenological component of yield.

Twenty-two cultivars were screened in order to assess the severity of peduncle inactivity in a number of genotypes and to determine a baseline for further investigations. For many cultivars, it was observed that very few of the potential reproductive sites managed to contribute to yield. In the most severe example (cultivar Vita-5) 60% of those peduncle sites which became productive failed to remain so. Mapping of the peduncle activity for this cultivar revealed that peduncle inactivity was attributable to the cessation of development, temporary suppression, or abscission, with only 17% of the vegetative nodes possessing an associated peduncle which contributed to yield (Section 2.3). For this cultivar, it was further observed that relatively little yield was contributed by the upper two thirds of the plant, despite the presence of several potential sites. This observation was quantified for all of the cultivars tested and was observed to be true for the majority of these. This led to the suggestion that the activities of the main stem may have limited the reproductive capacity of the lower third of the plants, which included the lower branches.

Based on the findings of the cultivar screening, two lines of research were conducted using the cultivar Vita-5. In the first of

these (Experiment Series I, Section 3), the effects of a number of chemical and manipulative treatments, known or thought to influence apical dominance were reported. Modification of apical meristem activity by such means generally had favorable effects on yield accretion or harvest indices over those of control plants (Section 3). One, though not both, of the studies conducted with 2,3,5-triiodobenzoic acid (TIBA) revealed an increase in all yield components and this was at least in part a reflection of increases in the number of peduncles which became and remained reproductive (Section 3.3).

Yield increases observed in the decapitation/benzyladenine treatments were not always a reflection of increases in the number of active peduncles. More often, these were due to increases in the amount of dry matter appropriated to reproductive components (Sectioon 3.6). Either actual increases in yield or increases in harvest indices over control plants were observed for the treatments in that study. Decapitation alone resulted in an increase in branching components, yields, and harvest indices, while overalll vegetative dry weight accumulation was reduced. Benzyladenine application to axillary buds following decapitation further increased branching components compared to decapitation alone and resulted in increased seed yields concommitant with increased vegetative yields. While foliar sprays of benzyladenine had no effect on branching unless combined with decapitation, and no significant effects on yield over that of controls were observed <u>per se</u>, harvest indices were increased by at least 30%. In addition to increased agronomic productivity which might be even more evident in

high-density field plantings, the picture presented presented in Plate 3 clearly demonstrates a more easily harvestable product for the foliar benzyladenine spray, with pods sitting well above the leaves.

All of the treatments in the decapitation/benzyladenine study led to a more agronomically efficient dry matter partitioning between reproductive and vegetative components, possibly by reducing competition for photoassimilates and nitrogen. Based on these findings, it was suggested that modifications of apical dominance through plant growth regulation might produce valuable yield increases for this cultivar and possibly others. Further, it was suggested that crop improvement might be achieved by selection for early branching. Such varietal differences in axillary bud development have been observed in tomato, for example (Tucker, 1979).

While some of the findings of Experiment Series I_o lent support to the view that greater yield accretion might be realized by a reduction in competition for plant resources in favor of reproductive components, the findings of Experiment Series II (Section 4) put forward a model of competitive inhibition between reproductive components themselves. Having demonstrated variations in the ability of a sink to attract assimilates (with a three-day old pod, for example, accumulating greater proportions of ^{14}C than a flower), and having suggested that this might be due to hormonal gradients, it was observed that a competitively strong enough reproductive (or created) sink could sequester large amounts of ^{14}C-assimilates from a source generally associated with another reproductive unit (Section 4.4). Similarly, for studies on competition between between two wheat ears with differing grain numbers

but receiving assimilates from a common source leaf, it was observed that in the short term the ear with a larger number of grains drew a disproportionately large share of its resources from the source leaf equidistant from both ears (Cook and Evans, 1978). Both the findings of this latter study and the one conducted here are consistent with the notion that a rapidly growing sink generates a greater flow from more distant sources than does a weakly growing competing sink (Gifford and Evans, 1981). Hence, in light of the possibility of the existence of such 'competitive inhibition', a greater yield potential might be realizable by a greater synchrony of peduncle development, with competing sinks of similar strengths achieved by genetic selection or chemical manipulation.

Two limiting processes to yield accretion in this cowpea cultivar might be implied by the findings of this study, notably that of unfavorable effects on yield accretion due to apical dominance and that of arrested, suppressed, or ceased peduncle activity due to competitive inhibition by stronger sinks.

Over the course of these experiments, the author has become aware of possible investigations that would contribute to the understanding of yield-limiting processes in cowpea, and suggests that the following research be considered, as extensions to the studies reported here.

The treatments of the decapitation/benzyladenine studies might be extended over a number of genotypes, both determinate and indeterminate, and in various environments, including tropical field conditions, in order to better elucidate the interaction of apical dominance and yield. This would be of particular interest with nodulated plants, since

nodulation has been observed to promote branching (Summerfield *et al.*, 1978), possibly *via* cytokinin production.

As the internodal competition study can serve only as a model of what might occur in intact plants, it would be of interest to investigate 'competitive inhibition' on a whole plant basis. At reproductive units of differing activity, endogenous hormone production might be studied, and more exact quantitative tracer techniques than those used here might be employed to determine 'sink strength'. The author recommends that, for these latter types of studies, a known quantity of tracer material be supplied to plants, in order to facilitate and strengthen data analysis.

6. REFERENCES

Accati, E.G., L. Basoccu and S. Sulis. 1980. Effect of 6-benzyladenine and other cytokinins on flower production of spray carnations. Acta Hortic. 91: 115-121.

Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean Phaseolus vulgaris. Crop Sci. 7: 508-516.

Adams, M.W. 1974. Plant architecture and yield in grain legumes. Rep. TAC/FAO working party on grain legumes. New Dehli, India, 21 pp.

Adedipe, N.O. and D.P. Ormrod. 1975. Absorption of foliar-applied E@P by successive leaves and distribution patterns in relation to early fruiting and abscission in the cowpea (Vigna unguiculata L.) Ann. Bot. (Lond.) 39: 639-646.

Adedipe, N.O., R.A. Fletcher and D.P. Ormrod. 1976. Distribution of ^{14}C assimilates in the cowpea (Vigna unguiculata L.) in relation to fruit abscission and treatment with benzyladenine. Ann. Bot. (Lond.) 40: 731-737.

Adedipe, N.O., L.A. Hunt and R.A. Fletcher. 1971. Effects of benzyladenine on photosynthesis, growth, and senescence of the bean plant. Physiol. Plant. 25: 151-153.

Ali, A. and R.A. Fletcher. 1971. Hormonal interaction in controlling apical dominance in soybeans. Can. J. Bot. 49: 1727-1731.

Aronoff, S. 1955. Translocation from soybean leaves. II. Plant Physiol. 30: 184-185.

Ashley, D.A. 1972. ^{14}C-labelled photosynthate translocation and utilization in cotton plants. Crop Sci. 12: 69-742.

Basnet, B.S., G.M. Paulsen and C.D. Nickell. 1972. Growth and compostion responses of soybeans to some growth regulators. Agron. J. 64: 550-552.

Batch, J.J. 1981. Recent developments in growth regulators for cereal crops. Outlook Agric. 10: 371-378.

Bauer, M.E., J.W. Pendleton, J.E. Beuerlein and S.R. Ghorashy. 1976. Influence of terminal bud removal on the growth and yield of soybeans. Agron. J. 68: 709-711.

Bauer, M.E., T.G. Sherbeck and A.J. Ohlrogge. 1969. Effects of rate, time, and method of application of TIBA on soybean production. Agron. J. 61: 604-606.

Biggs, T. 1982. Vegetables. The Royal Horticultural Society's Encyclopedia of Practical Gardening. Mitchell Beazley Publishers Ltd., 96 pp.

Bimie, R.C. and P.E. Clifford. 1980. Effects of some defoliation and decapitation treatments on the productivity of french beans. Ann. Bot. 46: 811-813.

Booth, A., J. Moorby, C.R. Davies, H. Jones and P.F. Wareing. 1962. Effects of indoyl-3-acetic acid on the movement of nutrients within plants. Nature (Lond.) 194: 204-205.

Boulter, D., M.I. Evans and A. Thompson. 1973. Protein quality, pp. 239-249. Proc. first I.I.T.A. Grain Legumes Improvement Workshop, I.I.T.A., Nigeria.

Brevedan, R.I., D.B. Egli and J.E. Leggett. 1978. Influence of N nutrition on flower and pod abortion and yield of soybean. Agron. J. 70: 81-84.

Brown, K. J. 1968. Translocation of carbohydrates in cotton: movement to the fruiting bodies. Ann. Bot. 32: 703-714.

Bunt, A.C. 1976. Modern Potting Composts. The Pennsylvania State University Press, University Park, 277pp.

Burrows, W.J. and D.J. Carr. 1970. Cytokinin content of pea seeds during their growth and development. Physiol. Plant. 23: 1064-1070.

Burt, R.L. 1964. Carbohydrate utilization as a factor in plant growth. Aust. J. Biol. Sci. 17: 867-877.

Burton, J.C. and R.C. Curley . 1966. Influence of triiodobenzoic acid on growth, nodulation and yields of inoculated soybeans. Agron. J. 58: 406-408.

Campbell, R.E. and J.K. Greig. 1974. Selected growth regulators increase yield of snapbeans. Hortscience 9: 71-72.

Carmi, A. and D. Koller. 1978. Effects of the roots on the rate of photosynthesis in primary leaves of bean (Phaseolus vulgaris L.). Photosynthetica 12: 178-184.

Carmi, A. and D. Koller. 1979. Regulation of photosynthetic activity in the primary leaves of bean (Phaseolus vulgaris L.) by materials moving in the water-conducting system. Plant. Physiol. 64: 285-288.

Carpenter, W.J. and W.H. Carlson. 1972. The effect of growth regulators on chrysanthemums. J. Am. Soc. Hortic. Sci. 97: 349-351.

Carpenter, W.J. and R.C. Rodriguez. 1971. The effect of plant growth regulating chemicals on rose shoot development from basal and axillary buds. J. Am. Soc. Hortic. Sci. 96: 389-391.

Carpenter, W.J., R.C. Rodriguez and W.H. Carlson. 1971. Growth regulator induced branching of non-pinched pointsettias. Hortscience 6: 457-458.

Carpenter, W.J., R.C. Rodriguez and W.H. Carlson. 1972. Improved geranium branching with growth regulator sprays. Hortscience 7: 291-292

Catalino, M. and J.A. Hill. 1969. Interaction between gibberellic acid and kinetin in overcoming apical dominance, natural and induced by IAA, in tomato (Lycopersicon esculentum. Mill. cv Potentale). Nature (Lond.) 222: 985-986.

Chan, B.G. and J.C. Cain. 1967. The effect of seed formation on subsequent flowering in apple. Proc. Am. Soc. Hort. Sci. 91: 63-68.

Chowdhury, J.U., Q.A. Faltah and Z. Husain. 1978. Yield response of three soybean varieties to TIBA application. Bangladesh J. Bot. 7: 93-96.

Clapp, J.G. 1973. Response of Bragg Soybean to TIBA (2,3,5-triiodobenzoic acid). Agron. J. 65: 41-43.

Clifford, P.E. 1979. Source limitation of sink yield in mung beans. Ann. Bot. 43: 397-399.

Cook, M.G. and L.T. Evans. 1978. Effect of relative sink and distance of competing sinks on the distribution of photosynthetic assimilates in wheat. Aust. J. Plant. Physiol. 5: 495-509

Crompton, H.J., C.P. Lloyd-Jones and D.G. Hill-Cottingham. 1981. Translocation of labelled assimilates following photosynthesis of $^{14}CO_2$ by the field bean Vicia faba. Physiol. Plant. 51: 189-194

Davey, J.E. and J. Van Staden. 1978. Cytokinin activity in Lupinus alba. 3. Distribution in fruits. Physiol. Plant. 43: 87-93.

Davies, C.R. and P.F. Wareing. 1965. Auxin-induced transport of radiophosphorus in stems. Planta (Berl.) 65: 139-156.

Davies, C.R., A.K. Seth and P.F. Wareing. 1966. Auxin and kinetin interaction in apical dominance. Science 151: 468-469

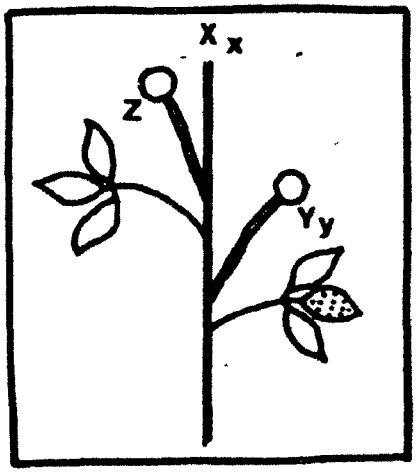
Egli, D.B. 1976. Planting date, row width, population, and growth regulators, pp. 56-62, in World Soybean Research (edited by L.D. Hill). Interstate, Illinois.

Egli, D.B. and J.E. Leggett. 1976. Rate of dry matter accumulation in soybeans with varying sink-source ratios. Agron. J. 68: 371-374.

Figure 10

^{14}C activity recovered by reproductive units of cowpea cv. Vita-5 subjected to various treatments (refer to Figure 8)

(means of 3 replicates)



X - ^{14}C activity found in reproductive units expressed as % of total activity recovered by plant

x - standard error of X

Y - ^{14}C activity found in reproductive unit P1 expressed as % of total activity recovered by reproductive units

Z - ^{14}C activity found in reproductive unit P2 expressed as % of total activity recovered by reproductive units

y - standard error of Y and Z

El Baradi, T.A. 1975. Pulses: 1. Cowpeas. Abstr. Trop.Agric. 1(12): 9-19.

El Beltagy, A.S. and M.A. Hall. 1975. Studies on endogenous levels of ethylene and auxin in Vicia faba during growth and development. New Phytol. 75: 215-224.

Everat-Bourbouloux, A. and D. Charnay. 1982. Endogenous abscisic acid levels in stems and axillary buds of intact or decapitated broad-bean plants (Vicia faba L.). Physiol. Plant. 54: 440-445.

Ezedinma, F.O.C. 1973a. Effects of defoliation and topping on semi-upright cowpeas (Vigna unguiculata (L.) Walp.) in a humid tropical environment. Exp. Agric. 9: 203-207.

Ezedinma, F.O.C. 1973b. Partition of dry matter between vegetative and reproductive components of semi-upright cowpeas (Vigna unguiculata (L.) Walp.). Nigerian Agric. J. 10: 156-159.

Faber, W.R. and J.W. White. 1977. The effect of pruning and growth regulator treatments on rose plant renewal. J. Am. Soc. Hortic. Sci. 102: 223-225.

Flinn, A.M. and J.S. Pate. 1970. A quantitative study of carbon transfer from pod and subtending leaf to the ripening seeds of the field pea (Pisum arvense L.). J. Exp. Bot. 21: 71-82

Galston, A.W. 1947. The effect of 2,3,5-triiodobenzoic acid on the growth and flowering of soybeans. Am. J. Bot. 34: 356-360.

Geiger, D.R. 1966. Effect of sink region cooling on translocation of photosynthate. Plant. Physiol. 41: 1667-1672.

Gifford, R.M. and L.T. Evans. 1981. Photosynthesis, carbon partitioning, and yield. Ann. Rev. Plant Physiol. 32: 485-509.

Goodwin, P.B. and P.E. Cansfield. 1967. The control of branch growth on potato tubers. III. The basis of correlative inhibition. J. Exp. Bot. 18: 297-307.

Graham, P.H. 1978. Some problems and potentials of field beans (Phaseolus vulgaris) in Latin America. Field Crops Res. 1: 295-317.

Greer, H.A.L. and I.C. Anderson. 1965. Response of soybeans to triiodobenzoic acid under field conditions. Crop. Sci. 5: 229-232.

Gregory, P.G. and J.A. Veale. 1957. A reassessment of the problem of apical dominance. Symp. Soc. Exp. Biol. 11: 1-20

Haagen-Smit, A.J., W.B. Dandliker, S.H. Wittwer and A.E. Murneek. 1946. Isolation of 3-indole-acetic acid from immature corn kernels. Am. J. Bot. 33; 118-120.

Hale, C.R. and R.J. Weaver. 1962. The effect of developmental stage on direction of translocation of photosynthate in Vitis vinifera. Hilgardia 33: 89-131.

Hansen, W.R. and R.M. Shibles. 1978. Seasonal log of the flowering and podding activity of field-grown soybeans. Agron. J. 70: 47-50.

Hardman, L.L. 1970. The effects of some environmental conditions on flower production and pod set in soybean Glycine max (L.) Merrill var. Hark. Diss. Abstr. 31: 2401-B.

Hardy, R.W.F. 1978. Chemical plant growth regulation in world agriculture, pp. 165-206, in Plant regulation and world agriculture (edited by T. Scott). NATO advanced study institute series volume 22.

Harvey, D.M. 1973. The translocation of ^{14}C-photosynthate in Pisum sativum L. Ann. Bot. 37: 787-794.

Harris, G.P. and B. Jeffcoat. 1972. Distribution of ^{14}C-labelled assimilates in flowering carnation plants. J. Hortic. Sci. 47: 25-35.

Hatch, A.H. and L.E. Powell. 1971. Hormone-directed transport of ^{32}P in Malus sylvestris seedlings. J. Am. Soc. Hortic. Sci. 96: 230-234.

Hay, J.R. 1956. The effect of 2,4-dichlorophenoxyacetic acid and 2,3,5-triiodobenzoic acid on the transport of indoleacetic acid. Plant Physiol. 31: 118-120.

Hicks, D.R., J.W. Pendleton, and W.O. Scott. 1967. Response of soybeans to TIBA (2,3,5-triiodobenzoic acid) and high fertility levels. Crop Sci. 7: 397-398.

Hipp, B.W. and W.R. Cowley. 1969. Influence of 2,3,5-triiodobenzoic acid and gibberellin on growth, yield and nutrient content in Southern peas. J. Am. Soc. Hortic. Sci. 94: 269-271.

Huff, A. and C.D. Dybing. 1980. Factors affecting shedding of flowers in soybean (Glycine max (L.) Merrill). J. Exp. Bot. 31: 751-762.

Hume, D.J. and J.G. Criswell. 1973. Distribution and utilization of ^{14}C-labelled assimilates in soybeans. Crop Sci. 13: 519-524.

Hume, D.J., J.W. Tanner and J.G. Criswell. 1972. Effects of environment on response of soybeans to TIBA. Crop Sci. 12: 293-294.

Huxley, P.A. and R.J. Summerfield. 1976. Photomorphogenetic effects of lamp type on growth of some species of tropical grain legumes in controlled environment growth cabinets. Plant Sci. Lett. 6: 25-33.

Ishag, H.M. 1970. Growth and yield of irrigated groundnuts (Arachis hypogea L.) grown at differing spacing in Sudan Gezira. J. Agric. Sci. 74: 533-537.

Isley, D. 1982. Leguminosae and Homo sapiens. Econ. Bot. 36: 46-70.

Ismail, A.M.A. and G.R. Sagar. 1981. The influence of leaf age, leaf position, and sinks on the rate of export and partition of ^{14}C at different stages of development following assimilation of $^{14}CO_2$ by a single leaf of Vicia faba L. J. Hortic. Sci. 56: 55-63.

Jackson, E.K. 1975. Increased yield of carnation cuttings and flowers by treatment with ACCEL plant growth regulator. Hortscience 10: 309.

Jackson, E.K. and J.C. Dingle. 1971. The use of the cytokinin SD 8339 (PBA) for branching floricultural crops. Hortscience 6: 288.

Jain, H.K. and K.L. Mehra. 1980. Evoultion, adaptation, relationships, and uses of the species of Vigna cultivated in India, pp. 459-468, in Advances in Legume Science (edited by R.J. Summerfield and A.H. Bunting), Royal Botanic Gardens, Kew.

Jeffcoat, B. 1977. Influence of the cytokinin, 6-benzylamino-9-(tetrahydropyran-2-yl)-9H-purine, on the growth and development of some ornamental crops. J. Hortic. Sci. 52: 143-153.

Jeffcoat, B. and G.P. Harris. 1972. Hormonal regulation of the distribution of ^{14}C-labelled assimilates in the flowering shoot of carnation. Ann. Bot. (Lond.) 36: 353-361.

Johnson, R.M. and W.D. Raymond. 1964. The chemical composition of some tropical plants. 2. Pigeon peas (Cajanus cajan) and cowpeas (Vigna unguiculata). Trop. Sci. 6: 68-73.

Katagiri, K. and H. Tsuji. 1980. Increase in DNA content of primary leaves of Phaseolus vulgaris upon decapitation. J. Exp. Bot. 31: 209-222.

Khan, A.A. and G.R. Sagar. 1966. Distribution of ^{14}C-labelled products of photosynthesis during the commercial life of the tomato crop. Ann. Bot. (Lond.) 30: 727-743.

Kipps, A. and D. Boulter. 1973. Carbon transfer from the bloom node leaf to the fruit of Vicia faba L. New Phytol. 72: 1293-1297.

Kuo, C. G., M.C.H. Jung and S.C.S. Tsou. 1978. Translocation of ^{14}C-photosynthate in mung bean during the reproductive period. Hortscience 13: 580-581.

Lawes, D.A. 1974. Field beans: improving yield and reliability. SPAN 17: 21-23.

Leopold, A.C. and M. Kawase. 1964. Benzyladenine effects on bean leaf growth and senescence. Am. J. Bot. 51: 294-298.

Leopold, A.C., E. Niedergang-Kamien and J. Janick. 1959. Experimental modification of plant senescence. Plant Physiol. 34: 570-573.

Linck, A.J. and T.W. Sudia. 1960. Transport specificity of ^{14}C to the fruit of Pisum. Plant Physiol. 35(suppl.),iii.

Linck, A.J. and T.W. Sudia. 1962. Translocation of labelled photosynthate from the bloom node leaf to the fruit of Pisum sativum. Experentia (Basel) 18: 69-70.

Lovell, P.H. 1969. Interrelationships of cotyledonary shoots in Pisum sativum. Physiol. Plant. 22: 506-515.

Lovell, P.H. and P.J. Lovell. 1970. Fixation of CO_2 and export of photosynthate by the carpel in Pisum sativum. Physiol. Plant. 23: 316-322.

Lovett Doust, J. and G.W. Eaton. 1982. Demographic aspects of flower and fruit production in bean plants Phaseolus vulgaris L. Am. J. Bot. 69: 1156-1164

Lucas, E.O., G.M. Milbourn, and P.N. Whitford. 1976. The translocation of ^{14}C photosynthate from leaves and pods in Phaseolus vulgaris. Ann. Appl. Biol. 83: 285-290.

Lush, W.M. and L.T. Evans. 1981. The domestication and improvement of cowpeas (Vigna unguiculata (L.) Walp.). Euphytica 30: 579-587.

Mahin, D.T. and R.T. Lofberg. 1966. A simplified method of sample preparation for determination of tritium, carbon-14 or sulfur-35 in blood or tissue by liquid scintillation counting. Anal. Biochem. 16: 500-509.

Malik, N.S.A. and A.M.M. Berrie. 1975. Correlative effects of fruits and leaves in senescence of pea plants. Planta 124: 169–175.

Meidner, H. 1970. Effects of photoperiodic induction and debudding in Xanthium pennsylvanicum and of partial defoliation in Phaseolus vulgaris on rates of net photosynthesis and stomatal conductance. J. Exp. Bot. 21: 164–169.

Mothes, K. and L. Englebrecht. 1961. Kinetin-induced transport of substances in excised leaves in the dark. Phytochemistry (Oxf.) 1: 58–62.

Narayanan, A. and A.R. Sheldrake. 1976. Pulse physiology - Annual Report 1974–1975 - Part I - Pigeonpea physiology, I.C.R.I.S.A.T., Hyderabad, India. 77pp.

National Academy of Sciences. 1979. Tropical legumes: resources for the future. National Academy of Sciences, Washington, D.C., 328 pp.

Newaz, M.A. and D.A. Lawes. 1980. Diferential response of Vicia faba L. genotypes to 2,3,5-triiodobenzoic acid (TIBA). Euphytica 29: 419–424.

Niedergang-Kamien, E. and A.C. Leopold. 1957. Inhibitors of polar auxin transport. Physiol. Plant. 10: 29–38.

Niedergang-Kamien, E. and F. Skoog. 1956. Studies on polarity and auxin transport in plants. I. Modification of polarity and auxin transport by triiodobenzoic acid. Physiol. Plant. 9: 60–73.

Nitsch, J.P. 1955. Free auxins and free tryptophan in the strawberry. Plant Physiol. 30: 33–39

Ohkawa, K. 1979. Promotion of renewal canes in greenhouse roses by 6-benzylaminopurine without cutback. Hortscience 14:612–613.

Ojehomon, O.O. 1968a. The development of the inflorescence and extra-floral nectaries of Vigna unguiculata (L.) Walp. J. W. Afr. Sci. Assoc. 13: 92–110.

Ojehomon, O.O. 1968b. Flowering, fruit production and abscission in cowpea Vigna unguiculata (L.) Walp. J. W. Afr. Sci. Assoc. 13: 227-234.

Ojehomon, O.O. 1970. Effect of continuous removal of open flowers on the seed yield of two varieties of cowpea Vigna unguiculata (L.) Walp. J. Agr. Sci. 74: 375-381.

Ojehomon, O.O. 1972. Fruit abscission in cowpeas, Vigna unguiculata (L.) Walp. I. Distribution of ^{14}C-assimilates in the inflorescence, and comparative growth of ovaries from persisting and abscising open flowers. J. Exp. Bot. 23: 751-761.

Ojehomon, O.O. 1975. Fruit abscission in cowpea, Vigna unguiculata (L.) Walp. II. Quantitative estimationsof total nucleic acids in ovaries of persisting and abscising flowers. J. Exp. Bot. 26: 921-926.

Ojehomon, O.O., A.S. Rathjen and D.G. Morgan. 1968. Effect of daylength on the morphology and flowering of five determinate varieties of Phaseolus vulgaris L. J. Agric. Sci. 71: 209-214.

Olufajo, O.O., R.W. Daniels and D.H. Scarisbrick. 1982. The effect of pod removal on the translocation of ^{14}C photosynthate in Phaseolus vulgaris L. cv. Lochness. J. Hortic. SCi. 57: 333-338.

Okelana, M.A.O. and N.O. Adedipe. 1982. Effects of gibberellic acid, benzyladenine, and 2-chloroethylphosphonic acid (CEPA) on growth and fruit asbscission in the cowpea (Vigna unguiculata L.). Ann. Bot. (Lond.) 49: 485-491.

Pate, J.S. and A.M. Flinn. 1977. Fruit and seed development , pp. 431-468, The physiology of the garden pea, (edited by J.F. Sutcliffe and J.S. Pate), Academic Press, London.

Patrick, J.W. and P.F. Wareing. 1972. Experiments on the mechanism of hormone-directed transport., pp. 695-700, Plant growth substances, 1970. Springer-Verlag, Berlin.

Patrick, J.W. and P.F. Wareing. 1973. Auxin-induced transport of metabolites in stems of Phaseolus vulgaris L. J. Exp. Bot. 24: 1158-1171.

Patrick, J.W. and P.F. Wareing. 1976. Auxin-promoted transport of metabolites in stems of Phaseolus vulgaris L., Effects at the site of application. J. Exp. Bot. 27: 969-982.

Phillips, I.D.J. 1969. Apical dominance. pp. 124-162, in The physiology of plant growth and development, (edited by M.B. Wilkins), London: McGraw-Hill.

Phillips, I.D.J. 1971. Factors influencing the distribution of growth between stem and axillary buds in decapitated bean plants. J. Exp. Bot. 22: 465-471.

Phillips, I.D.J. 1975. Apical dominance. Annu. Rev. Plant Physiol. 26: 341-367.

Phillips, D.R., R.F. Horton and R.A. Fletcher. 1969. Ribonuclease and chlorophyllase activities in senescing leaves. Physiol. Plant. 22: 1050-1054.

Platt, B.S. 1962. Tables of representative values of foods commonly used in tropical countries. Spec. Rep. Sev. Med. Res. Comm., U.K., 302.

Porter, N.G. 1977. The role of abscissic acid in flower abscission of Lupinus luteus. Physiol. Plant. 40: 50-84

Porter, N.G. and R.F.M. van Stevenick. 1966. An abscission-promoting factor in Lupinus luteus (L.). Life Sci. 5: 2301-2308.

Purseglove, E.L. 1968. Tropical crops: dicotyledons. Longmans, London, 719 pp.

Rachie, K.O. and L.M. Roberts. 1974. Grain legumes of the lowland tropics. Adv. Agron. 26: 1-132.

Reddy, P.R. and A.A. Zaheda. 1979. Influence of TIBA on productivity and short term incorporation of ^{32}P in pigeon pea (Cajanus cajan (L.) Millsp.). J. Nucl. Agric. Biol. 8: 19-21.

Russell, W.J. and D.R. Johnson. 1975. Translocation patterns in soybeans exposed to $^{14}CO_2$ at four different time periods of the day. Crop Sci. 15: 75-77.

Ryan, G.F. 1974. Chemicals to induce branching of Photinia 'Fraseri' and Rhododendron Exbury azaleas. Hortic. Sci. 9:534-535.

Sachs, T. and K.V. Thimann. 1964. Release of lateral buds from apical dominance. Nature (Lond.) 201: 939-940.

Sachs, T. and K.V. Thimann. 1967. The role of auxins and cytokinins in the release of buds from dominance. Am. J. Bot. 54: 136-144.

Sant'Anna, R., A.J. Ohlrogge, J.E. Christian and C.E. Breckenridge. 1970. Foliar absorption and distribution of 2,3,5-triiodobenzoic acid (TIBA) in soybeans (Glycine max). Agron. J. 62: 731-736.

Saxena, N.P. and A.R. Sheldrake. 1976. Pulse physiology annual report, 1974-1975, Part II. Chickpea physiology, I.C.R.I.S.A.T., Hyderabad, India, 55pp.

Schaeffer, G.W. and F.T. Sharpe, Jr. 1969. Release of axillary bud inhibition with benzyladenine in tobacco. Bot. Gaz. 130: 107-110.

Schmitt, B.A. 1979. Protein, calories and development: nutritional variables in the economies of developing countries. Westview Press, Boulder, Coloradao. 312pp.

Scott, R.A. and J.L. Liverman. 1956. Promotion of leaf expansion by kinetin and benzylaminopurine. Plant Physiol. 31: 321-322.

Seth, A.K. and P.F. Wareing. 1967. Hormone-directed transport of metabolites and its possible role in plant senescence. J. Exp. Bot. 18: 65-77.

Shein, T. and D.I. Jackson. 1971. Hormone interaction in apical dominance in Phaseolus vulgaris L. Ann. Bot. 35: 555-564.

Sinha, S.K. 1977. Food legumes: distribution, adaptability and biology of yield. FAO plant production and protection paper no. 3, Food and Agriculture Organization of the United Nations; Rome, 124 pp.

Sinha, S.K. and M.C. Ghildiyal. 1973. Increase in yield of bengal gram (Cicer arietinum L.) by 2,3,5-triiodobenzoic acid. Crop Sci. 13:283

Shimshi, E.E. 1966. A rapid field method for measuring photosynthesis with labelled carbon dioxide. J. Exp. Bot. 20: 381-401.

Smith, B.W. 1954. Arachis hypogaea. Reproductive efficiency. Am. J. Bot. 41: 607-616.

Stecher, P.G. (editor). 1968. The Merck Index, 8th edition, Merck and Co., Rahway, N.J.

Steele, W.M. and K.L. Mehra. 1978. Structure, evolution, and adaptation to farming systems and environments in Vigna, pp 393-404, Advances in Legume Sciences (edited by R.J. Summerfield and A.H. Bunting), Royal Botanic Gardens, Kew.

Stewart, K.A. 1976. On the yield of cowpea. Ph. D. Thesis, University of Reading. 124 pp.

Stewart, K.A., R.J. Summerfield, F.R. Minchin and B.J. Ndunguru. 1980. Effects of contrasting aerial environments on yield potential in cowpea (Vigna unguiculata (L.) Walp.). Trop. Agric. 57: 43-52.

Summerfield, R.J. and H.C. Wien. 1980. The effects of photoperiod and air temperature on growth and yield of economic legumes, pp. 17-36, in Advances in Legume Science, (edited by R.J. Summerfield and A.H. Bunting) Royal Botanic Gardens, Kew.

Summerfield, R.J., P.A. Huxley, and F.R. Minchin. 1977. Plant husbandry and management techniques for growing grain legumes under simulated tropical conditions in controlled environments. Exp. Agric. 13: 81-92.

Summerfield, R.J., P.A. Huxley, and W. Steele. 1974. Cowpea (Vigna unguiculata (L.) Walp.). Field Crop Abstr. 27: 301-312.

Summerfield, R.J., F.R. Minchin, and E.H. Roberts. 1978. Realisation of yield potential in soybean (Glycine max (L.) Merr.) and cowpea (Vigna unguiculata (L.) Walp.), pp 125-134, in Proceedings BCPC/BPGRG Symposium on opportunities for chemical plant growth regulation. British crop protection council monograph no. 21.

Summerfield, R.J., F.R. Minchin, E.H. Roberts, and P. Hadley. 1983. Cowpeas,in Potential productivity of field crops under different environments (edited by S. Yoshida), I.R.R.I., the Philippines. (In press)

Tamas, I.A., J.L. Ozbun, D.H. Wallace, L.E. Powell, and C.J. Engels. 1979a. Effect of fruit on dormancy and abscisic acid concentration in the axillary buds of Phaseolus vulgaris L. Plant Physiol. 64: 615-619.

Tamas, I.A., D.H. Wallace, P.M. Ludford, and J.L. Ozbun. 1979b. Effect of older fruits on abortion and abscisic acid concentration of younger fruits in Phaseolus vulgaris L. Plant Physiol. 64: 620-622.

Tanner, J.W. and S. Ahmed. 1974. Growth analysis of soybeans treated with TIBA. Crop Sci. 14: 371-374.

Tayo, T.O. 1980. The response of two soya-bean varieties to the loss of apical dominance at the vegetative stage of growth. J. Agric. Sci., 95: 409-416.

Tayo, T.O. 1982. Growth, development and yield of pigeon pea (Cajanus cajan (L.) Millsp.) in the lowland tropics. 3. Effect of early loss of apical dominance. J. Agric. Sci., 98: 79-84.

Thimann, K.V. and F. Skoog. 1933. Studies on the growth hormone of plants. III. The inhibiting action of the growth substance on bud development. Proc. Nat. Acad. Sci., USA 19: 714-716.

Thimann, K.V. and F. Skoog. 1934. On the inhibition of bud development and other functions of growth substances in Vicia faba. Proc. Roy. Soc. Ser. B., Biol. Sci. 114: 317-339.

Tucker, D.J. 1979. Axillary bud development in the tomato. Ann. Bot. (Lond.) 43: 393-395.

Van Schaik, P.H. and A.H. Probst. 1958a. The inheritance of inflorescence type, peduncle length, flowers per node, and percent flower shedding in soybeans. Agron. J. 50: 98-102.

Van Schaik, P.H. and A.H. Probst. 1958b. Effects of some environmental factors on flower production and reproductive efficiency in soybeans. Agron. J. 50: 192-197.

Van Staden, J. and A. Carmi. 1982. The effects of decapitation on the distribution of cytokinins and growth of Phaseolus vulgaris plants. Physiol. Plant. 55: 39-44.

Van Stevenick, R.F.M. 1957. Factors affecting the abscission of reproductive organs of yellow lupines (Lupinus luteus L.). I. The effects of different patterns of flower removal. J. Exp. Bot. 8: 373-381.

Van Stevenick, R.F.M. 1958. Factors affecting the abscission of reproductive organs of yellow lupines (Lupinus luteus L.). II. The effects of growth substances, defoliation, and removal of lateral growth. J. Exp. Bot. 9: 372-383

Van Stevenick, R.F.M. 1959. Factors affecting the abscission of reproductive organs of yellow lupines (Lupinus luteus L.). III. Endogenous growth substances in virus-infected and healthy plants and their effect on abscission. J. Exp. Bot. 10: 367-376

Wareing, P.F. 1978. Growth regulation and assimilate partition, pp. 309-317, in Plant regulation and world agriculture (edited by T.K. Scott); Plenum Press, N.Y.

Wareing, P.F., M.M. Khalifa and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220: 453-457.

Wax, L.M., and J.W. Pendleton. 1968. Influence of 2,3,5-triiodobenzoic acid (TIBA) on soybeans planted in different cultural systems. Agron. J. 60: 425-427.

Webb, J.A. and P.R. Gorham. 1964. Translocation of photosynthetically assimilated ^{14}C in straight-necked squash. Plant. Physiol. 39: 663-672.

Webster, B.D., M.E. Craig and C.L. Tucker. 1975. Effects of ethephon on abscission of vegetative and reproductive structures of Phaseolus vulgaris L. Hortscience 10: 154-156.

Weigle, J.L., M.L. Robbins, A.R. Beck and K.M. Batal. 1973. Influence of growth regulators on pod set and yield in snap beans and related crops. Hortscience 8: 35-36.

Wickson R.D. and K.V. Thimann. 1958. The antagonism of auxin and kinetin in apical dominance. Physiol. Plant. 11: 62-74.

Wiebold, W.J., D.A. Ashley and H.R. Boerma. 1981. Reproductive abscission levels and patterns for eleven determinate soybean cultivars. Agron. J. 73: 43-46.

Wien, H.C., S.L. Altschuler, J.L. Ozbun and D.H. Wallace. 1976. ^{14}C assimilate distribution in Phaseolus vulgaris L. during the reproductive period. J. Am. Soc. Hortic. Sci. 101: 510-513.

Williams, A.M. and N.G. Marinos. 1977. Regulation of the movement of assimilate into ovules of Pisum sativum cv. Greenfast: Effect of pod temperature. Aust. J. Plant Physiol. 4: 515-521.

Williams, A.M. and R.R. Williams. 1978. Regulation of movement of assimilate into ovules of Pisum sativum cv. Greenfast: A 'remote' effect of the pod. Aust. J. Plant. Physiol. 5: 295-300.

Williams, R.D. 1964. Assimilation and translocation in perennial grasses. Ann. Bot. 28: 419-426.

Wolfe, T.K. and M.S. Kipps. 1959. Production of field crops; McGraw-Hill, New York, fifth edition, 424 pp.

Woolley, D.J. and P.F. Wareing. 1972. The interaction between growth promotors in apical dominance. II. Environmental effects on endogenous cytokinin and gibberellin levels in Solanum andigena. New Phytol. 71: 1015-1025.

Yeang, H.Y. and J.R. Hillman. 1982. Lateral bud outgrowth in Phaseolus vulgaris and the levels of ethylene in the bud and adjacent tissue. J. Exp. Bot. 33: 111-117.

Yoshida, S. 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23: 437-464.

Zwar, J.A. and A.H.G.C. Rijven. 1956. Inhibition of transport of indole-3-acetic acid in the etiolated hypocotyl of Phaseolus vulgaris. Aust. J. Biol. Sci. 9: 528-538.

Appendix A Analysis of variance: Cultivar screening (Section 2)

Plant attributes recorded:

1. Days to emergence
2. Days to anthesis
3. Days to harvest
4. Peduncle number
5. Percent non-functional peduncle sites
6. Pods per plant
7. Seeds per pod
8. Mean seed weight
9. Seed weight (g/plant)

1.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	24.86	1.13	2.39	0.0252	15.05
Error	21	9.93	0.47			
Corrected total	43	34.80				

Source	df	SS	F
Treatment	21	24.30	2.45*
Block	1	0.57	1.20

2.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	892.27	40.56	5.69	0.0001	5.34
Error	21	149.63	7.13			
Corrected total	43	1041.91				

Source	df	SS	F
Treatment	21	891.91	5.96***
Block	1	0.05	0.05

3.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	2147.95	97.63	7.48	0.0001	4.47
Error	21	273.93	13.04			
Corrected total	43	2421.87				

Source	df	SS	F
Treatment	21	2141.39	7.82***
Block	1	6.57	0.50

4.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	1275.50	57.98	5.13	0.0002	17.27
Error	21	237.47	11.31			
Corrected total	43	1512.98				

Source	df	SS	F
Treatment	21	1179.48	4.97***
Block	1	96.02	8.49**

5.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	8334.15	378.83	7.96	0.0001	20.79
Error	21	999.23	47.58			
Corrected total	43	9333.39				

Source	df	SS	F
Treatment	21	8323.42	8.33***
Block	1	10.74	7.42*

6.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	657.23	29.87	6.63	0.0001	12.61
Error	21	94.66	4.51			
Corrected total	43	751.89				

Source	df	SS	F
Treatment	21	653.39	6.90***
Block	1	3.84	0.37

7.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	266.35	12.11	5.59	0.0001	12.18
Error	21	45.51	2.17			
Corrected total	43	311.86				

Source	df	SS	F
Treatment	21	256.48	5.64***
Block	1	9.87	4.55*

8.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	62058.08	2820.82	21.72	0.0001	9.06
Error	21	2726.90	129.85			
Corrected total	43	64784.97				

Source	df	SS	F
Treatment	21	61988.28	22.73***
Block	1	69.80	0.54

9.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	22	1933.53	87.89	7.25	0.0001	14.45
Error	21	254.52	12.12			
Corrected total	43	2188.05				

Source	df	SS	F
Treatment	21	1923.93	7.24***
Block	1	9.60	0.63

* = significant at p=0.05
** = significant at p=0.01
*** = significant at p=0.001

Appendix B1.1 Analysis of variance: TIBA pilot study (Section 3.3)

Plant attributes recorded:

1. Number of active peduncles per plant
2. Number of pods per plant
3. Number of seeds per pod
4. Number of seeds per plant
5. Mean seed weight (mg)
6. Seed weight (g) per plant

1.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	92.13	15.36	4.95	0.021	17.15
Error	8	24.80	3.10			
Corrected total	14	116.93				

Source	df	SS	F
Treatment	4	69.60	5.61*
Block	2	22.53	3.63

2.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	185.07	30.84	7.2	0.0068	15.14
Error	8	34.27	4.28			
Corrected total	14	219.33				

Source	df	SS	F
Treatment	4	167.33	9.77**
Block	2	17.73	2.07

3.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	9.88	1.65	0.80	0.60	14.84
Error	8	16.43	2.05			
Corrected total	14	26.31				

Source	df	SS	F
Treatment	4	2.98	0.36
Block	2	6.90	1.68

4.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	19178.93	3196.49	2.75	0.09	25.68
Error	8	9314.80	1164.35			
Corrected total	14	28493.73				

Source	df	SS	F
Treatment	4	14810.40	3.18
Block	2	4368.53	0.21

5.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	2802.33	467.06	0.70	0.66	21.59
Error	8	5372.29	671.54			
Corrected total	14	8174.62				

Source	df	SS	F
Treatment	4	1192.15	0.44
Block	2	1610.18	

6.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	6	268.22	44.70	1.16	0.41	38.62
Error	8	309.35	38.67			
Corrected total	14	577.57				

Source	df	SS	F
Treatment	4	229.79	1.49
Block	2	38.43	0.50

* = significant at p = 0.05
** = significant at p = 0.01

Appendix B1.2 Correlation coefficients: TIBA pilot study (Section 3.3)

Plant attributes:

1. (PED/PL): Number of active peduncles per plant
2. (POD/PL): Number of pods per plant
3. (S/POD): Number of seeds per pod
4. (S/PL): Number of seeds per plant
5. (MSW): Mean seed weight
6. (SW): Seed weight (g) per plant

	POD/PL	S/POD	S/PL	MSW	SW
PED/Pl	0.90**	-0.09	0.65**	-0.39	0.63*
POD/PL		0.18	0.88***	-0.28	0.77***
S/POD			0.60*	-0.19	0.58***
S/PL				-0.28	0.90***
MSW					-0.65**

* = significant at p = 0.05
** = significant at p = 0.01
*** = significant at p= 0.001

Appendix B2 Analysis of variance: TIBA study
(Section 3.4)

Plant attributes recorded:

1. Number of active peduncles per plant
2. Number of pods per plant
3. Number of seeds per pod
4. Number of seeds per plant
5. Mean seed weight (mg)
6. Seed weight (g) per plant
7. Number of branches per plant
8. Number of nodes per plant
9. Number of nodes arising from branches per plant
10. Number of main stem nodes
11 Aerial vegetative dry weight (g) per plant

1.

Source of variation	df	SS	MS	F	C.V.
Model	1	6.13	6.13	1.62	50.25
Error	6	22.75	3.79		
Corrected total	7	28.88			

2.

Source of variation	df	SS	MS	F	C.V.
Model	1	6.13	6.13	1.62	47.21
Error	6	22.75	3.79		
Corrected total	7	28.88			

3.

Source of variation	df	SS	MS	F	C.V.
Model	1	0.02	0.02	0.00	39.05
Error	6	51.83	8.64		
Corrected total	7	51.85			

4.

Source of variation	df	SS	MS	F	C.V.
Model	1	171.13	171.13	10.95	14.57
Error	6	93.75	15.63		
Corrected total	7	264.88			

5.

Source of variation	df	SS	MS	F	C.V.
Model	1	1843.81	1843.81	7.45	11.71
Error	6	1485.77	247.63		
Corrected total	7	3329.58			

6.

Source of variation	df	SS	MS	F	C.V.
Model	1	0.33	0.33	1.92	11.74
Error	6	1.04	0.17		
Corrected total	7	1.37			

7.

Source of variation	df	SS	MS	F	C.V.
Model	1	0.00	0.00	0.00	16.33
Error	6	4.00	0.67		
Corrected total	7	4.00			

8.

Source of variation	df	SS	MS	F	C.V.
Model	1	6.13	6.13	1.48	12.60
Error	6	24.75	4.13		
Corrected total	7	30.88			

9.

Source of variation	df	SS	MS	F	C.V.
Model	1	10.13	10.13	2.67	37.99
Error	6	22.75	3.79		
Corrected total	7	32.88			

10.

Source of variation	df	SS	MS	F	C.V.
Model	1	1.13	1.13	1.80	6.52
Error	6	3.75	0.63		
Corrected total	7	4.88			

11.

Source of variation	df	SS	MS	F	C.V.
Model	1	0.08	0.08	0.01	19.79
Error	6	47.40	7.90		
Corrected total	7	47.48			

12. Source of variation	df	SS	MS	F	C.V.
Model	1	840.50	840.50	110.84	4.79
Error	6	45.50	7.58		
Corrected total	7	886.00			

Appendix B3 Analysis of variance: BA pilot study

Plant attributes recorded:

1. Number of active peduncles per plant
2. Number of pods per plant
3. Number of seeds per pod
4. Number of seeds per plant
5. Mean seed weight (mg)
6. Seed weight (g) per plant

1.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	39.58	4.40	1.37	0.29	31.15
Error	14	44.92	3.21			
Corrected total	23	84.50				

Source	df	SS	F
Block	2	7.75	1.21
Mode of application(M)	1	1.50	0.47
Concentration of BA(C)	3	28.17	2.93
M*C	3	2.17	0.23

2.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	75.92	8.44	1.09	0.42	32.35
Error	14	107.92	7.71			
Corrected total	23	183.83				

Source	df	SS	F
Block	2	8.08	0.52
Mode of application(M)	1	0.17	0.02
Concentration of BA(C)	3	64.17	2.77
M*C	3	3.50	0.15

3.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	56.98	6.33	1.62	0.2022	23.66
Error	14	54.76	3.91			
Corrected total	23	111.74				

Source	df	SS	F
Block	2	15.09	1.93*
Mode of application(M)	1	4.87	1.24
Concentration of BA(C)	3	29.96	2.55
M*C	3	7.06	0.60

4.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	8549.67	949.96	2.00	0.12	31.15
Error	14	6658.33	475.60			
Corrected total	23	15208.00				

Source	df	SS	F
Block	2	3991.00	4.20
Mode of application(M)	1	433.50	0.91
Concentration of BA(C)	3	1987.67	1.39
M*C	3	2137.50	1.50

5.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	904.21	100.47	0.62	0.76	8.71
Error	14	2274.26	162.45			
Corrected total	23	3178.47				

Source	df	SS	F
Block	2	697.69	2.15
Mode of application(M)	1	24.64	0.15
Concentration of BA(C)	3	95.68	0.20
M*C	3	86.20	0.18

6.

Source of variation	df	SS	MS	F	PR>F	C.V.
Model	9	139.99	15.55	2.22	0.09	26.27
Error	14	97.92	6.99			
Corrected total	23	237.92				

Source	df	SS	F
Block	2	54.76	3.91
Mode of application(M)	1	14.52	2.08
Concentration of BA(C)	3	38.07	1.81
M*C	3	32.64	1.56

* = significant at p = 0.05

Appendix B4.1 Analysis of variance: Decapitation/benzyladenine study (Section 3.6)

Plant attributes recorded:

1. Number of branches per plant
2. Number of vegetative nodes originating from branches per plant
3. Number of nodes per branch per plant
4. Number of active peduncles per plant
5. Number of pods per plant
6. Number of seeds per pod
7. Number of seeds per plant
8. Mean seed weight (mg)
9. Seed weight (g) per plant
10. Aerial vegetative dry weight (g) per plant
11. Total aerial dry weight (g) per plant
12. Final node number per plant
13. Number of nodes appearing after treatment per plant
14. Harvest index
15. Height (cm)

1.

Source of variation	df	SS	MS	F	C.V.
Model	4	12.70	3.18	1.80	31.65
Error	15	26.50	1.77		
Corrected total	19	39.20			

2.

Source of variation	df	SS	MS	F	C.V.
Model	4	443.20	110.80	24.53***	23.75
Error	15	66.75	4.52		
Corrected total	19	510.95			

3.

Source of variation	df	SS	MS	F	C.V.
Model	4	15.54	3.89	20.54***	21.33
Error	15	2.84	0.19		
Corrected total	19	18.38			

4.

Source of variation	df	SS	MS	F	C.V.
Model	4	5.30	1.33	1.02	33.54
Error	15	19.50	1.30		
Corrected total	19	24.80			

5.

Source of variation	df	SS	MS	F	C.V.
Model	4	13.50	3.38	1.79	28.89
Error	15	28.25	1.88		
Corrected total	19	41.75			

6.

Source of variation	df	SS	MS	F	C.V.
Model	4	72.55	18.14	6.76**	27.41
Error	15	40.25	2.68		
Corrected total	19	112.80			

7.

Source of variation	df	SS	MS	F	C.V.
Model	4	818.30	204.58	25.26***	10.99
Error	15	121.50	8.10		
Corrected total	19	939.80			

8.

Source of variation	df	SS	MS	F	C.V.
Model	4	1153.26	288.31	1.39	9.77
Error	15	3121.94	208.13		
Corrected total	19	4275.19			

9.

Source of variation	df	SS	MS	F	C.V.
Model	4	10.34	2.59	13.77***	11.51
Error	15	2.82	0.19		
Corrected total	19	13.16			

10.

Source of variation	df	SS	MS	F	C.V.
Model	4	150.84	37.71	13.46***	15.64
Error	15	42.01	2.80		
Corrected total	19	192.85			

11. Source of variation	df	SS	MS	F	C.V.
Model	4	176.26	44.07	14.97***	11.86
Error	15	44.15	2.94		
Corrected total	19	220.41			

12. Source of variation	df	SS	MS	F	C.V.
Model	4	325.30	81.33	12.51***	16.55
Error	15	97.50	6.50		
Corrected total	19	422.80			

13. Source of variation	df	SS	MS	F	C.V.
Model	4	311.70	77.93	16.35***	20.22
Error	15	71.50	4.77		
Corrected total	19	383.20			

14. Source of variation	df	SS	MS	F	C.V.
Model	4	499.60	124.90	8.42***	14.35
Error	15	222.48	14.83		
Corrected total	19	722.08			

15. Source of variation	df	SS	MS	F	C.V.
Model	4	7002.00	1750.50	86.95***	7.61
Error	15	302.00	20.13		
Corrected total	19	7304.00			

** = significant at p = 0.01
*** = significant at p =0.001

Appendix B4.2 Correlation coefficients: Decapitation/ benzyladenine study: yield components (Section 3.6)

Plant attributes:

1. (PED/PL): Number of active peduncles per plant
2. (POD/PL): Number of pods per plant
3. (S/POD): Number of seeds per pod
4. (S/PL): Number of seeds per plant
5. (MSW): Mean seed weight
6. (SW): Seed weight (g) per plant

	POD/PL	S/POD	S/PL	MSW	SW
PED/PL	-0.11	0.37	0.38	-0.22	0.41
POD/PL		-0.73***	0.02	0.22	0.14
S/POD			0.60**	-0.49*	0.49*
S/PL				-0.59**	0.93***
MSW					-0.27

* = significant at p = 0.05
** = significant at p = 0.01
*** = significant at p= 0.001

Appendix B4.3 Correlation coefficients: Decapitation/ benzyladenine study: vegetative and yield attributes (Section 3.6)

Plant attributes:

1. (VEG/PL): Aerial vegetative dry weight per plant
2. (DW /PL): Total dry weight (g) per plant
3. (NN/PL): Final node number per plant
4. (NNT/PL): Number of nodes appearing after treatment per plant
5. (HI): Harvest index

	DW/PL	NN/PL	NNT/PL	HI
VEG/PL	0.97***	0.72***	0.68***	-0.75***
DW/PL		0.77***	0.74***	-0.59**
NN/PL			0.95***	-0.41
NNT/PL				-0.37

* = significant at p = 0.05
** = significant at p = 0.01
*** = significant at p= 0.001

Appendix C1. The effect of time on the distribution of ^{14}C assimilates from a leaf fed $^{14}CO_2$

AC1.1 Objectives A preliminary experiment was conducted in order determine a suitable time for photosynthate distribution to the plant parts under study.

AC1.2 Materials and Methods Plants with three-day old pods present at the third node were used and pruned to one leaf, one peduncle, and one pod, according to the specifications outlined in Section 4.2. As described, the single fed leaf on each plant was exposed to $^{14}CO_2$ for ten minutes. In this experiment, the patterns of ^{14}C translocation were studied after (a) 6 hour and (b) 24 hour light periods. The full photoperiods were opted for, as it is generally considered necessary to do this in order to prevent confounding the effects of translocation with those that occur due to the time of day (Russell and Jackson, 1975; Wein et al., 1976). The two treatments were replicated three times each.

AC1.3 Results and Discussion Results are presented in Table 10 and Appendix C 7. After 6 hours, nearly 70% of ^{14}C incorporated by the single leaf had been retained by this leaf and only approximately 10%, 8%, and 12% of the total recovered activity was located in the pod, peduncle, and stem tissues, respectively. Over 24 hours,

Table 10. Distribution of recovered activiety (% of total) in plants at 6 and 24 hours following $^{14}CO_2$ exposure to a single leaf

Plant parts	% of total recovered activity	
	after 6 hours	after 24 hours
leaf	69.22 (2.3)	29.93 (1.3)
stem	11.94 (2.2)	12.67 (2.3)
peduncle	8.42 (0.7)	19.46 (1.6)
pod	10.41 (0.8)	37.94 (1.1)

figures represent the means of 3 observations.
standard error in brackets.

however, over 70% of the ^{14}C incorporated by the single fed leaf had moved out of this leaf, and much greater proportions had moved into the reproductive unit (peduncle + pod) located in the leaf's axil. While a similar proportion for stem accumulation was observed for periods of 6 and 24 hours, the longer translocation period allowed for a greater proportion of the ^{14}C assimilates to be accumulated by the peduncle and the pod (2.3 and 3.6-fold increases, respectively).

Based on the observation of increased movement of photoassimilates to the reproductive unit after 24 hours, this time period was used for subsequent studies.

Appendix C2. The effect of a black plastic barrier over the peduncle on the distribution of ^{14}C from a fed leaf

AC2.1 Objectives As organs such as the peduncle are characteristically photosynthetic, it was felt that the photosynthetic contribution of the pedunle might differentially affect ^{14}C distribution from one plant to another by 'dilution' of the ^{14}C contribution to the peduncle stumps and reproductive organs. Hence, a preliminary test was conducted in order to ascertain the effects of a black plastic barrier designed to alleviate light interception by the peduncle.

AC2.2 Materials and methods Plants with three-day old pods present at the third node were used and pruned to leave one leaf, one peduncle, and one pod according to the specifications outlined in Section 4.2. As described, the single leaf on each plant was exposed to $^{14}CO_2$ for ten minutes. In this experiment, the patterns of ^{14}C translocation were studied when (a) peduncles were left as is; and (b) when they were covered by a black plastic barrier (large black straws - 0.7 cm diameter milkshake straws which were spray painted black and cut to the required peduncle length).

AC2.3 Results and discussion Results are presented in Table 12 and Appendix C8. Similar proportions of ^{14}C were exported from the leaf in both instances. Where a black plastic barrier was present, greater

Table 11. Distribution of recovered activity (% of total) in plant parts, with or without a black plastic barrier over the peduncle, 24 hours following $^{14}CO_2$ exposure to a single leaf.

Plant parts	% of total recovered activity	
	with black plastic barrier	without black plastic barrier
leaf	29.59 (1.0)	29.92 (1.3)
stem	9.12 (1.3)	12.67 (2.3)
peduncle	16.97 (2.5)	19.46 (1.6)
pod	44.31 (2.1)	37.94 (1.1)

figures represent the means of three observations.
standard error in brackets.

quantities of ^{14}C-assimilates were diverted to the reproductive organs (peduncles + pods), though the difference was minor. Hence, since the effects on ^{14}C distribution were negligible, if such differences did exist, the black plastic barrier was used in subsequent experiments, in order to alleviate undue variability. The similarity of response also allowed for reasonable estimation of the veritable effects of subsequent treatments had no such barrier been present.

Appendix C3 Means analysis : mobilizing potential study
(Section 4.3;Figure 7)

Trt.	Plant Part	Mean	Standard deviation	Standard error of mean	Sum	Variance	C.V. (%)
A.	Stem	3.1301	1.0638	1.6142	9.3903	1.1316	33.99
	Leaf	35.2294	0.6912	0.3991	105.6882	0.4778	1.96
	Peduncle unit	61.6405	1.6986	0.9807	184.9215	2.8853	2.76
B.	Stem	23.5322	2.3313	1.3460	70.5967	5.4350	9.91
	Leaf	41.4890	3.7940	2.1905	124.4669	14.3948	9.15
	Peduncle unit	34.9788	4.0111	2.3158	104.9363	16.0888	11.47
C.	Stem	45.5621	13.0964	7.5612	136.6862	171.5160	28.74
	Leaf	53.8781	13.3106	7.6849	161.6342	177.1731	24.71
	Peduncle unit	0.5598	0.2148	0.1240	1.6796	0.0461	38.36
D.	Stem	23.8429	5.3867	3.1100	71.5286	29.0169	22.59
	Leaf	70.3500	6.4361	3.7159	211.0500	41.4240	9.15
	Peduncle unit	5.8071	1.0515	0.6071	17.4214	1.1057	18.11
E.	Stem	24.9873	7.5479	4.3578	74.9620	56.9718	30.21
	Leaf	53.4610	16.5782	9.5714	160.3831	274.8379	31.01
	Peduncle unit	21.5516	9.2973	5.3678	64.6549	86.4401	43.14
F.	Stem	27.3290	2.7989	1.6160	81.9870	7.8340	10.24
	Leaf	66.1310	4.1305	2.3848	198.34926	17.0611	6.25
	Peduncle unit	6.5401	4.8463	2.7980	19.6204	23.4868	74.10

means are that of three observations

Appendix C4.1 Means analysis : internodal competition study
(Section 4.4; Figure 9)

Trtmt.	Plant Part	Mean	Standard deviation	Standard error of mean	Sum	Variance	C.V. (%)
I.a	Stem	9.5827	1.8956	1.0944	28.7481	3.5931	19.78
	L1	38.2496	8.7294	5.0399	114.7487	76.2020	22.82
	L2	9.0035	0.8157	0.4710	27.0105	0.6654	9.06
	P1	37.8682	6.6830	3.8584	113.6046	44.6622	17.65
	P2	5.2960	1.2452	0.7189	15.8880	1.5506	23.51
I.b	Stem	18.2220	2.6054	1.5042	54.6660	6.7880	14.30
	L1	66.2378	9.9300	5.7331	198.7135	98.6040	14.99
	L2	5.8948	1.2296	0.7099	17.4425	1.3054	19.38
	P1	6.8416	3.6194	2.0897	20.5247	13.1002	52.90
	P2	2.8039	3.4899	2.0149	8.4116	12.1798	124.47
I.c	Stem	14.6434	3.0193	1.7432	43.9302	9.1164	20.62
	L1	76.9592	2.9808	1.7211	230.8777	8.8862	3.87
	L2	5.8142	1.2296	0.7099	17.4425	1.5120	21.15
	P1	2.3930	0.4477	0.2585	7.1789	0.2004	18.71
	P2	0.1902	0.1116	0.6443	0.5706	0.0125	58.67
II.a	Stem	8.7055	3.4353	1.9834	26.1166	11.8013	39.46
	L1	37.8177	2.3372	1.3494	113.4531	5.4627	6.18
	L2	3.3186	1.4963	0.8639	9.9559	2.2389	45.09
	P1	48.8464	5.9212	3.4186	146.5393	35.0602	12.12
	P2	1.3117	0.5525	0.3190	3.9350	0.3052	42.18
II.b	Stem	8.4622	2.1275	1.2283	25.3866	4.5264	25.14
	L1	65.5916	3.6753	2.1219	187.7748	13.5079	5.87
	L2	1.5963	1.3055	0.7537	4.7889	1.7043	81.78
	P1	25.1216	0.6936	0.4004	75.3648	0.4810	2.76
	P2	2.2283	2.2584	1.3039	6.6850	5.1002	101.35

II.c	Stem	11.3144	1.6788	0.9628	33.9832	2.8185	14.84
	L1	65.2377	3.8542	2.2252	195.7132	14.8549	5.91
	L2	8.9031	3.5287	2.0373	26.7093	12.4519	39.64
	P1	12.7340	3.8634	2.2305	38.2018	14.9260	30.34
	P2	1.8108	0.7824	0.4517	5.4325	0.6122	43.21
III.a	Stem	39.2914	6.7064	3.8719	117.8741	44.9759	17.07
	L1	43.1781	5.5845	3.2242	129.5342	31.1870	12.93
	L2	4.3176	0.8643	0.4990	12.9527	0.7471	20.02
	P1	0.7617	0.3856	0.2227	2.2850	0.1487	50.63
	P2	12.4513	1.5986	0.9229	37.3540	2.5554	12.84
III.b	Stem	28.6355	1.8506	1.0684	85.9065	3.4246	6.46
	L1	31.1540	3.3088	1.9104	93.4619	10.9484	10.62
	L2	6.5621	3.0972	1.7882	19.6863	9.5929	47.20
	P1	14.6913	6.8588	3.9599	44.0738	47.0425	46.87
	P2	18.9572	0.7961	0.4596	56.8715	0.6337	4.20
III.c	Stem	21.1508	5.6254	3.2478	63.4525	31.6451	26.60
	L1	71.2962	4.1106	2.3732	213.8885	16.8967	5.77
	L2	3.2020	1.4825	0.8559	9.6061	2.1977	46.30
	P1	3.4592	0.5085	0.2936	10.3776	0.2586	14.70
	P2	0.8918	0.4813	0.2779	2.6753	0.2317	53.98
IV.	Stem	13.4751	11.8097	6.8183	40.4253	139.4685	87.64
	L1	28.4391	2.6537	1.5321	85.3174	7.0423	9.33
	L2	12.8384	16.3616	9.4464	38.5151	267.7032	127.44
	P1	14.2502	6.1018	3.5229	42.7507	37.2324	42.82
	P2	30.9972	3.5071	2.0248	92.9915	12.2995	11.31

means are that of three obeervations

Appendix C4.2 Means analysis : internodal competition study (Section 4.4; Figure 10)

Trtmt.	Plant Part	Mean	Standard deviation	Standard error of mean	Sum	Variance	C.V. (%)
I.a	P1	87.8187	0.7515	0.4339	263.4560	0.5647	0.86
	P2	12.1813	0.7515	0.4339	36.5440	0.5647	6.17
I.b	P1	77.7140	14.0401	8.1061	233.1421	197.1249	18.10
	P2	22.2860	14.0401	8.1061	66.8579	197.1249	63.00
I.c	P1	92.5242	4.0430	2.3342	277.5730	16.3459	4.37
	P2	7.4758	4.0430	2.3342	22.4273	16.3459	54.08
II.a	P1	97.3114	1.3541	0.7818	291.9342	1.8337	1.39
	P2	2.6886	1.3541	0.7818	8.0658	1.8337	50.37
II.b	P1	92.3542	7.0036	4.0435	277.0627	49.0510	7.58
	P2	7.6458	7.0036	4.0435	22.9373	49.0510	91.60
II.c	P1	87.5132	4.5614	2.6335	262.5397	20.8066	5.21
	P2	12.4868	4.5614	2.6335	37.4603	20.8066	36.53
III.a	P1	5.5717	1.9667	1.1355	16.7152	3.8680	35.30
	P2	94.4283	1.9667	1.1355	283.2848	3.8680	2.08
III.b	P1	41.7708	12.5543	7.2482	125.3125	157.6113	30.06
	P2	58.2292	12.5543	7.2482	174.6875	157.6113	21.56

III.c.	P1	79.9883	8.4020	4.8510	239.9649	70.5943	10.50
	P2	20.0117	8.4020	4.8510	60.0351	70.5943	41.99
	P1	38.2036	3.8191	2.2050	114.6107	14.5852	9.99
	P2	61.7964	3.8190	2.2050	185.3893	14.5852	6.18

means are that of three observations

Appendix C5 **Unanalyzed data: mobilizing potential study (Section 4.3)**

Trt.	rep.	recovered activity (dpm ^{14}C)				% of total recovered activity		
		stem	leaf	peduncle unit	Total	stem	leaf	peduncle unit
A	1	332	3478	5647	9457	3.51	36.78	59.71
	2	524	9343	17086	26953	1.94	34.67	63.39
	3	693	7043	12373	20109	3.45	35.02	61.53
B	1	1377	2066	1845	5288	26.04	39.07	34.89
	2	4451	8827	5969	19247	23.13	45.86	31.01
	3	1920	3542	3497	8959	21.43	39.54	39.03
C	1	2249	2366	29	4644	48.43	50.95	0.63
	2	4102	8974	42	13118	31.27	68.41	0.32
	3	8840	6558	114	15512	56.98	42.28	0.73
D	1	1587	3333	370	5290	30.00	63.01	6.99
	2	1458	5468	364	7290	20.00	75.01	4.99
	3	2183	7406	551	10140	21.53	73.04	5.43
E	1	839	3727	572	5138	16.33	72.54	11.13
	2	3187	4783	2589	10559	30.18	45.30	24.52
	3	1338	2001	1364	4703	28.45	42.55	29.00
F	1	1577	4264	682	6523	24.18	65.37	10.46
	2	1440	3593	57	5090	28.29	70.59	1.12
	3	2818	5960	768	9546	29.52	62.44	8.05

Appendix C6.1 Unanalyzed data: internodal competition study (Section 4.4, Figure 9)

Trt	rep	Recovered activity (dpm ^{14}C)						% of total recovered activity				
		Stem	L1	L2	P1	P2	Tot.	Stem	L1	L2	P1	P2
1.a	1	684	3688	688	2316	296	7672	8.92	48.07	8.97	30.19	3.86
	2	1169	3129	981	4095	599	9973	11.72	31.37	9.84	41.06	6.01
	3	851	3704	861	4444	632	10492	8.11	35.30	8.21	42.36	6.02
1.b	1	1163	5651	452	305	52	7623	15.26	74.13	5.93	4.00	0.68
	2	1716	4693	598	930	582	8519	20.14	55.09	7.02	10.92	6.83
	3	1481	5342	364	431	69	7687	19.27	69.49	4.74	5.61	0.90
1.c	1	1335	7343	692	183	16	9569	13.95	76.74	7.23	1.91	0.17
	2	749	3092	216	103	13	4173	17.95	74.10	5.18	2.47	0.31
	3	1178	7838	493	274	9	9292	12.03	80.04	5.03	2.80	0.09
2.a	1	1057	6579	519	10381	186	18722	5.65	35.14	2.77	55.45	0.99
	2	779	3761	485	4557	96	9678	8.05	38.86	5.01	47.09	0.99
	3	892	2833	156	3160	140	7181	12.42	39.45	2.17	44.01	1.95
2.b	1	1105	10675	129	3927	140	15976	6.92	66.82	0.81	24.58	0.88
	2	593	3276	169	1355	53	5446	10.89	60.15	3.10	24.88	0.97
	3	751	6043	87	2566	479	9906	7.58	60.80	0.88	25.90	4.84

2.c	1	981	5733	537	1537	227	9015	10.88	63.59	5.96	17.05	2.52
	2	745	3535	725	543	110	5658	13.17	62.48	12.81	9.60	1.94
	3	673	4737	540	786	66	6802	9.89	69.64	7.94	11.55	0.97
3.a	1	1995	1892	241	29	578	4735	42.13	39.96	5.09	0.61	12.21
	2	2795	4385	299	106	1251	8836	31.63	49.63	3.38	1.20	14.16
	3	3171	2872	322	34	790	7189	44.11	39.95	4.48	0.47	10.99
3.b	1	716	789	167	486	527	2685	26.67	29.39	6.22	18.10	19.63
	2	2692	3103	871	603	1604	8873	30.34	34.97	9.82	6.80	18.08
	3	2684	2703	339	1781	1780	9287	28.90	29.11	3.65	19.18	19.17
3.c	1	2300	7301	311	399	146	10457	21.99	69.82	2.97	3.82	1.40
	2	1143	5729	361	278	33	7544	15.15	75.94	4.79	3.69	0.44
	3	2094	5423	147	229	67	7960	26.31	68.13	1.85	2.88	0.84
4.	1	163	1865	1915	437	1819	6199	2.63	30.09	30.89	7.05	29.34
	2	2384	3106	424	1850	3020	10784	22.11	28.81	3.93	17.15	28.00
	3	1330	1862	208	1334	2533	7267	18.30	25.62	2.86	18.36	34.85

Appendix C6.2 Unanalyzed data: internodal competition study (Section 4.4; Figure 10)

Treatment	rep	recovered activity (dpm ^{14}C)			% of total recovered activity	
		P1	P2	P1+P2	P1	P2
I.a	1	2316	296	2612	88.67	11.33
	2	4095	599	4694	87.24	12.76
	3	4444	632	5076	87.55	12.45
I.b	1	305	52	357	85.43	14.57
	2	930	582	1512	61.51	38.49
	3	431	69	500	86.20	13.80
I.c	1	183	16	199	91.96	8.04
	2	103	13	116	88.79	11.21
	3	274	9	283	96.82	3.18
II.a	1	10381	186	10567	98.24	1.76
	2	4557	96	4653	97.94	2.06
	3	3160	140	3300	95.76	4.24
II.b	1	3927	140	4067	96.56	3.44
	2	1355	53	1408	96.24	3.76
	3	2566	479	3045	84.27	15.73
II.c	1	1537	227	1764	87.13	12.87
	2	543	110	653	83.15	16.85
	3	786	66	852	92.25	7.75

III.a	1	29	578	607	4.78	95.22
	2	106	1251	1357	7.81	92.19
	3	34	790	824	4.12	95.87
III.b	1	486	527	1013	47.98	52.02
	2	603	1604	2207	27.32	72.68
	3	1781	1780	3561	50.01	49.99
III.c	1	399	146	545	73.21	26.79
	2	278	33	311	89.39	10.61
	3	229	67	296	77.37	22.64
IV.	1	1819	2499	4318	42.13	57.87
	2	1850	3020	4870	37.99	62.01
	3	1334	2533	3867	34.50	65.50

Appendix C7 Unanalyzed data and means analysis: time/distribution study (Appendix C1)

Trt	rep	recovered activity (dpm ^{14}C)					% of total recovered activity			
		stem	leaf	peduncle	pod	total	stem	leaf	peduncle	pod
6 h.	1	839	4629	596	609	6673	12.57	69.37	8.93	9.13
	2	355	3308	322	543	4528	7.84	73.06	7.11	11.99
	3	1328	5619	794	871	8612	15.42	65.25	9.22	10.11
24h.	1	812	2157	1636	2630	7235	11.22	29.81	22.61	36.35
	2	999	1613	1016	2177	5805	17.21	27.79	17.50	37.50
	3	636	2134	1212	2650	6632	9.59	32.18	18.28	39.96

Treatment	plant part	mean	standard deviation	standard error of mean	sum	variance	c.v. (%)
6 hours	stem	11.9445	3.8290	2.2107	35.8335	14.6613	32.06
	leaf	69.2239	3.9072	2.2558	207.6718	15.2663	5.64
	peduncle	8.4208	1.1432	0.6600	25.2625	1.3069	13.58
	pod	10.4107	1.4558	0.8405	31.2322	2.1192	13.98
24 hours	stem	12.6741	4.0116	2.3161	38.0224	16.0928	31.65
	leaf	29.9257	2.1976	1.2688	89.7771	4.8295	7.34
	peduncle	19.4632	2.7545	1.5903	58.3895	7.5871	14.15
	pod	37.9370	1.8423	1.0636	113.8110	3.3939	4.86

Appendix C8 Unanalyzed data and means analysis: black plastic barrier study (Appendix C2)

Barrier	rep	recovered activity (dpm ^{14}C)					% of total recovered activity			
		stem	leaf	peduncle	pod	total	stem	leaf	peduncle	pod
+	1	933	2507	1299	3322	8061	11.57	31.10	16.11	41.21
	2	558	1942	849	3129	6478	8.61	29.98	13.11	48.30
	3	643	2483	1945	3893	8964	7.17	27.70	21.70	43.43
-	1	812	2157	1636	2630	7235	11.22	29.81	22.61	36.35
	2	999	1613	1016	2177	5805	17.21	27.79	17.50	37.50
	3	636	2134	1212	2650	6632	9.59	32.18	18.28	39.96

Black plastic barrier	plant part	mean	standard deviation	standard error of mean	sum	variance	c.v. (%)
+	stem	9.1204	2.2439	1.2955	27.3612	5.0349	24.60
	leaf	29.5928	1.7328	1.0004	88.7784	3.0026	5.86
	peduncle	16.9728	4.3598	2.5171	50.9184	19.0080	25.69
	pod	44.3139	3.6274	2.0943	132.9420	13.1582	8.19
-	stem	12.6741	4.0116	2.3161	38.0224	16.0928	31.65
	leaf	29.9257	2.1976	1.2688	89.7771	4.8295	7.34
	peduncle	19.4632	2.7545	1.5903	58.3895	7.5871	14.15
	pod	37.9370	1.8423	1.0636	113.8110	3.3939	4.86